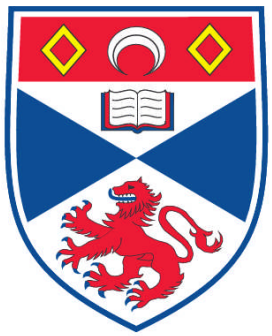
FUNCTIONAL DESIGN AND USE OF ACOUSTIC SIGNALS PRODUCED BY KILLER WHALES (*ORCINUS ORCA*)

Filipa Isabel Pereira Samarra

A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews



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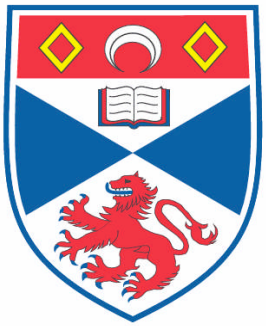

This thesis is submitted in partial fulfilment for the degree of PhD
at the
University of St Andrews

Submitted April 2011

Abstract

This study aimed to investigate possible functions of the sounds produced by herring-eating killer whales in the Northeast Atlantic.

In this study, I investigated the whistle repertoire of killer whales, which had previously only been studied in British Columbia, where it appeared to be restricted to the audible range. However, I show that high frequency whistles (> 17 kHz) were detected in Northeast Atlantic populations but not in Northeast Pacific populations. These results indicated substantial intraspecific variation in whistle production in killer whales. Little variation was observed in high frequency whistles recorded from three different sites in the Northeast Atlantic, suggesting this signal has a similar function across locations.

The estimated active space of high frequency whistles and burst-pulse calls suggested that these are short-range signals used for within-group communication. Source levels of burst-pulse calls were lower than what was previously described in British Columbia, which possibly reflected the fact that these sounds do not need to propagate far because distances between group members are generally short. Calls, high frequency whistles and herding calls produced at different depths did not appear to suffer effects due to increased pressure, such as changing frequency or duration characteristics.

Feeding appeared to take place below 10 m of depth, as suggested by the localisation of depth of production of feeding-related sounds. These depths were consistent with those at which tailslaps were produced in Dtags attached to individual whales. Feeding periods were characterised by deep diving, increased sound production and highly non-directional movement. These findings suggested that killer whales in a herring spawning ground use a feeding strategy different from carousel feeding used in herring overwintering grounds.

These findings showed that Northeast Atlantic killer whales have a different sound repertoire to other populations, and suggested that they may employ different feeding strategies depending on prey behaviour.

Declarations

1. Candidate's declarations

I, Filipa Isabel Pereira Samarra, hereby certify that this thesis, which is approximately 33,135 words in length, has been written by me, that it is the record of work carried out by me and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in January 2007 and as a candidate for the degree of Doctor of Philosophy in January 2007; the higher study for which this is a record was carried out in the University of St Andrews between 2007 and 2011.

Date: 4 October 2011 Signature of candidate:

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2. Supervisor's declaration

I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of Doctor of Philosophy at the University of St Andrews and that the candidate is qualified to submit this thesis in application for that degree.

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Acknowledgments

There are many people that I have to thank. I will start by thanking my supervisors Patrick Miller and John Harwood, they made most valuable comments to this thesis and I deeply appreciate their availability to review it in such a short time. I thank Patrick in particular for first introducing me to killer whales, by kindly allowing me to work with him during my Masters project. It was because he suggested I joined his fieldwork in Norway that many of my ideas to pursue this PhD developed. Patrick encouraged me since the beginning and it was through many stimulating discussions with him that many of the ideas discussed here developed.

This project was possible due to funding by a studentship from Fundação para a Ciência e a Tecnologia (grant SFRH/BD/30303/2006) and a Russell Trust Award (U. St Andrews).

Several people contributed with data that made part of Chapter 1. Thank you to Claire Lacey from the International Fund for Animal Welfare/The Song of the Whale Team who provided recordings from Iceland 2004, Marianne Rasmussen and Katja Vinding who provided high sampling frequency recordings from Iceland 2008 and Volker Deecke who provided recordings from West Coast Transients, British Columbia Residents and Shetland. The Dtag data from Norway 2005 was collected in collaboration with A. D. Shapiro. Florianne Plard, Annemike Podt and Matthew Eggleston helped with analysis of the Norway 2005, 2009 Dtag and Shetland data, respectively. Ricardo Antunes and H. Wood helped with localisation analysis conducted for Chapter 3.

Fieldwork was one of the most enjoyable parts of my project and I was lucky to do it with a bunch of really great people. These will be some of the fondest memories that I will keep and for that I am truly grateful to: Allan Ligon, Alex Fennell, Andy Foote, Annika Firmenich, Ari Shapiro, Hajime Yoshino, Hannah Williams, Hannah Wood, José Cervantes-Henriksen, Kagari Aoki, Katja Vinding, Marianne Rasmussen, Ralph Baylor, René Swift, Ricardo Antunes, Sanna Kuningas, Simon Moss, Volker Deecke and Yukihisa Kogure.

Although it was not part of the initial plan, I ended up doing most of this project in Iceland. Vestmannaeyjar is an amazing place with amazing people. Everyone at Café Kro welcomed me from the very first day and I have to thank in particular Simmi, Unnur and José who became, as they say, my Icelandic family. Páll Jónsson

was our collaborator, our captain and our friend. He provided all the logistic support in the Vestmannaeyjar Research Centre and I thank him immensely for making this such a nice project. I can only hope that this was the beginning of many more visits to Iceland.

With the past and present members of the Miller lab at the University of St Andrews I had great discussions and very good times both in and out of the office. Thank you especially to Catarina Alves, Eva Hartvig, Hajime Yoshino, Kagari Aoki Paul Wensveen and Ricardo Antunes.

Cláudia, Eva, Sanna, Marjolaine, Silvana and Catarina – thank you for always being there. With the Portuguese friends I had good food, good wine and good times. Obrigado pessoal! To my flatmates along the way Cormac, Sanna, Lewis and Silvana thank you for sharing the ups and downs of a PhD student's experience.

My dear friends Diana and Vera were there when it all began and are still a huge support today – obrigado migas! Together with Galésio and Coelho they made the visits back home even better!

Finally, I have to thank my family – without their support I probably would not have embarked in this journey. Mãe, pai, mano e avós, obrigado pelo apoio, carinho e por tudo o resto que as palavras não conseguem descrever.

Chapter 1

General Introduction

Signal design features

Acoustic communication occurs when one animal (the signaller) produces an acoustic signal conveying information that transmits through the environment and is detected by other animals (the receivers) (Bradbury & Vehrencamp, 1998). The receiver then uses the information to help make a decision on how it should respond and its response will affect the fitness of both the signaller and the receiver (Bradbury & Vehrencamp, 1998). Often communication involves a network of multiple signallers and receivers (McGregor & Peake, 2000).

The function of an acoustic signal can be defined as the adaptive consequences of communication (Smith, 1968, 1977). However, the same signal may have different functions depending on the receiver (Marler, 1961). For example, acoustic advertisement signals produced by males are used by females in mate choice and by other males in male-male interactions (Gerhardt & Huber, 2002). If signal production benefits signallers it may provide them with adaptive advantages. Thus, one can predict that signallers should evolve behaviours that entail production of appropriate signal types in the specific contexts in which the response of receivers provides a functional benefit to the signaller. Studying a species' vocal behaviour and repertoire of sound production in defined contexts therefore allows researchers to formulate hypotheses about the potential functions of different signals in a repertoire. This also aids in the interpretation of what information may be beneficial for signallers to transmit, how receivers might respond, and what specific benefits signallers ultimately gain by producing those signals.

Acoustic signals can be characterised by their frequency, time and amplitude. These design characteristics are shaped by the signal's function (Bradbury & Vehrencamp, 1998). For example, if a signal is produced to maintain contact between group members that disperse over a wide area, the signal's intensity and frequency should be appropriate to ensure it can be received over intended distances (e.g., Wahlberg et al., 2002). In contrast, signallers may produce lower amplitude and

higher frequency signals, which will be detectable only over shorter distances, if intended receivers are at close ranges and there is a cost to production of more intense signals (e.g., Dabelsteen et al., 1998). The characteristics of the environment in which communication takes place influence the degradation suffered by the signal before it reaches receivers (e.g., Marten & Marler, 1977). Signallers and receivers may also actively position themselves in locations and orientation postures that optimise information transfer (e.g., Holland et al., 1998; Brumm et al., 2011).

The design features of a signal may also have evolved to provide information to receivers about the signaller's quality and, for example, act in female mate choice (e.g., Gerhardt & Huber, 2002). Finally, the design of a signal is constrained by the capabilities of the signaller's sound production and the receiver's hearing mechanisms (Bradbury & Vehrencamp, 1998). Therefore, to fully understand the function of animal communication one has to take into account the environmental and social context in which communication occurs. Indeed, the selective pressures on signallers and receivers will depend on the context in which signals are produced (see review by Seyfarth & Cheney, 2003).

Observational studies provide baseline information about the contexts in which communication occurs. By recording the signals produced and the context they are produced in simultaneously, it is possible to develop hypotheses about the function of these signals (Slater, 1999). Ultimately these hypotheses should be tested by conducting playback experiments (e.g., Cheney & Seyfarth, 1982) to observe receivers' responses to signals. When the receiver's response to a particular signal is known, the information content of the signal can be inferred (Marler, 1961).

Over all but the shortest distances, acoustic communication is likely to be favoured over other signal modalities for transmitting information in the marine environment, because light attenuates rapidly in seawater and acoustic signals can be detected at greater ranges than any other signal modality (e.g., Tyack, 2000a). The selective pressures acting on animals living in such an environment are very different from those acting on terrestrial animals, making aquatic animals particularly interesting for studies of the function of acoustic signals, despite the increased difficulty in observing them. Among aquatic species, cetaceans have some of the most complex communication systems known (Tyack, 2000b).

Functional design of cetacean signals

The study of cetacean bioacoustics started in 1949, when the first recording of a free-ranging beluga (*Delphinapterus leucas*) was made off Canada (Watkins & Wartzok, 1985). Since then, many species have been recorded and three main sound categories have been recognised: clicks, burst-pulse calls and tonal whistles.

Some of the broad contexts of signal production that have been identified in cetaceans include: maintenance of group cohesion and social bonds [e.g. bottlenose dolphin (*Tursiops truncatus*) signature whistles, Caldwell & Caldwell, 1965; Caldwell et al, 1990; Janik & Slater, 1998]; feeding, either to detect prey (odontocete clicks used in echolocation, Au, 1993) or to manipulate prey behaviour [e.g., bottlenose dolphin bray calls, Janik, 2000a; and humpback whale (*Megaptera novaeangliae*) trumpet-like calls, Jurasz & Jurasz, 1979; Sharpe, 2001]; and reproduction [e.g., humpback whale song, Payne & McVay, 1971; blue whale (*Balaenoptera musculus*) and fin whale (*Balaenoptera physalus*) low-frequency calls, Oleson et al, 2007; Croll et al, 2002].

The social context in which signals are produced is a fundamental consideration in the design of cetacean signals. For example, the low frequency calls produced by male blue and fin whales are acoustically quite different from the higher-frequency and complex male humpback whale song, although all are thought to function in reproduction. Croll et al. (2002) suggested that these differences in signal design were related to different reproductive behaviours. While humpback whales have well defined breeding areas where conspecifics congregate to breed, fin and blue whales disperse widely and specific breeding grounds cannot be determined (Croll et al, 2002; Clapham, 1996). These differences would, therefore, be expected to favour the use of lower frequency and longer-range signals by blue and fin whales, but not by humpback whales.

Environmental characteristics influence the signal design in many terrestrial species (see Brumm & Slabbekoorn, 2005 for a review of influences of environmental noise). In cetaceans, examples of such influences are the low-frequency whistles of the Amazon river dolphin (*Inia geoffrensis*), which are thought to be an adaptation to its noisier river habitat (Ding et al., 1995), or the way in which belugas change their click frequency according to the background noise characteristics of their environment (Au et al, 1985).

A growing concern about the effects of increasing human induced noise in the ocean has stimulated the study of its impact on cetaceans (Richardson et al, 1995). Deecke (2007) points out that the aim of many of the playback experiments conducted with cetaceans to date has been to examine the effects of anthropogenic noise. Observational studies have shown that some species appear to change the rate of signal production, the signal types produced or the frequency of signals when exposed to man-made noise (e.g., Lesage et al., 1999; Rendell & Gordon, 1999).

It is very likely that the sound production and hearing mechanisms of cetaceans impose some constraints on the signals they produce. However, these sound production mechanisms are not fully understood for many species. Sound production in odontocetes appears to occur in the nasal passages (Cranford et al, 1996; Cranford, 2000). However, whether resonators are present and what structures may be involved in sound production as resonators is still poorly understood (e.g., Ridgway et al., 1980). Furthermore, the increased ambient pressure at depth may have selected for information on individual identity to be encoded in the time-frequency contour of acoustic signals. This is because these are under the control of the signaller and are not affected by pressure effects (Tyack, 1997; Tyack & Miller, 2002). Although the effects of depth on sound production have been studied in only a few species (e.g., Ridgway et al., 2001; Jensen et al., 2011a), hearing abilities do not seem to be affected by increased pressure with depth (Ridgway et al., 2001). More detail on the mechanisms of sound production and reception is necessary if we are to understand how these mechanisms constrain signal design.

Within cetaceans, killer whales (*Orcinus orca*) are a particularly interesting species for the study of the function of signals because they produce a varied repertoire of signals in different contexts, the function of which is not completely understood.

Killer whales

Killer whales are the largest-bodied species within the Delphinidae family (Order Cetacea: Suborder Odontoceti). They are found in all of the world's oceans, although they are most commonly seen in temperate waters (Baird, 2000). A long-term study of Northeast Pacific killer whales, particularly those found off British Columbia, started in the 1970s, and most of the information on population and group structure, behaviour and acoustic communication in this species has been gathered there (Ford

et al., 2000). However, studies in other areas of the Pacific, Atlantic and Southern Oceans have shed additional light on the variety of behaviours of this species (e.g., Guinet, 1991; Pitman & Ensor, 2003; Tarasyan et al., 2005). Particularly in the North Pacific and in Antarctic waters, sympatric ecotypes have been recognised based on differences in their diet, morphology and behaviour (Ford et al., 2000; Pitman & Ensor, 2003; Burdin et al., 2005; Pitman et al., 2007). Despite these differences, initial studies on genetic differentiation between different populations of killer whales suggested little diversity worldwide (Hoelzel et al., 2002). However, recent studies that have sequenced the mitogenome of samples from wider geographical locations have suggested that there is sufficient genetic differentiation for different species to be recognised (Morin et al., 2010). Specifically, two ecotypes from the Antarctic (ecotypes B and C) as well as Northeast Pacific transient killer whales are recommended to become separate species (Morin et al., 2010).

Individual killer whales can be identified by means of photo-identification, using the unique natural marks in their dorsal fin and saddle patch (Bigg, 1982). Photo-identification allowed for each individual to be recognised and associations between individuals to be studied (Bigg, 1982; Bigg et al., 1990). Social structure appears to vary according to the prey upon which a population of killer whales specialize. For example, fish-eating resident killer whales live in matrilineal groups, composed of a female and her offspring, from which no dispersion of offspring of either sex is observed (Bigg et al., 1990). Closely related matrilines associate to form pods, which are defined as groups of killer whales that associate for 50% or more of their time, that can vary in size from less than 10 to tens of individuals (Bigg et al., 1990). On the other hand, mammal-eating transient killer whales have a more fluid social structure with smaller groups from which offspring can disperse (Bigg et al., 1990; Baird & Dill, 1996; Baird & Whitehead, 2000).

Prey density and abundance may also affect group size. For example, groups of herring-eating killer whales in Norway also seem to have a social structure based on matrilineal groups (Bisther & Vongraven, 1995), but group sizes in herring spawning grounds are slightly smaller than groups encountered in herring overwintering grounds (Similä & Ugarte, 1997), where herring school density is much higher than during spawning (Nøttestad et al., 1996). Studies in the Northwest Pacific have shown that resident-type killer whales form stable matrilineal units but associations between different units did not reflect kinship (Ivkovich et al., 2010). This shows the diversity

of killer whale behaviours and how studies of different populations can help us to understand the factors that may affect such diversity.

Feeding behaviour

As a species, killer whales are considered to be generalist predators because they are known to feed upon a variety of prey, including fish, marine mammals and birds (Hoyt, 1994). However different populations seem to specialise on particular types of prey. Group and individual feeding behaviours of killer whales usually reflect the type of prey they feed upon and the habitat where feeding takes place. For example, killer whales in Patagonia regularly strand intentionally in order to capture southern sea lions (*Otaria flavescens*) and southern elephant seals (*Miruonga leonina*; Lopez & Lopez, 1985; Hoelzel, 1991). The same strategy is seen in the Crozet Archipelago, but here only females strand, possibly due to the characteristics of the beaches in that area (Guinet, 1991). Because beaches were of a lower slope than those in Patagonia, it could be difficult for the large-sized males to strand without risk (Guinet, 1991). In Antarctica, killer whales create waves to wash resting seals off floating ice and into the water (Visser et al., 2008).

Fish-eating killer whales also show varied behaviours depending on the species of fish they feed upon. For example, resident killer whale groups off British Columbia spread out over large areas to search for salmon independently and may then share prey captured by one whale (Ford & Ellis, 2006). In contrast, fish-eating killer whales in Norway, Iceland and the Northwest Pacific feed upon schooling prey and use a group strategy called 'carousel feeding' to encircle their prey (Sigurjónsson et al. 1988; Similä & Ugarte, 1993; Tarasyan et al., 2005). Studies from all of these locations report that killer whales use underwater tailslaps to debilitate groups of prey, and then feed upon individual fish (Similä & Ugarte, 1993; Simon et al., 2005; Tarasyan et al., 2005).

Acoustic communication of killer whales

Like other cetaceans, killer whales produce three main categories of acoustic signals: clicks, whistles and burst-pulse calls (Schevill & Watkins, 1966; Ford, 1989; Thomsen et al., 2001). Clicks are short, broadband signals usually used in echolocation (Au et al., 2004). Whistles are tonal-like signals that are thought to be used in close-range communication during socialising (Thomsen et al., 2001, 2002).

Their low source levels and active space further support their proposed function in short-range communication (Miller, 2006). Burst-pulse calls are the most commonly produced sound and are composed of clicks emitted at high repetition rates (Ford, 1989). Burst-pulse calls that have a stereotyped time-frequency contour and can be organised into discrete categories are called discrete calls (Ford, 1989). Calls are produced in all behavioural contexts and, although the rate of production of different call types can change between contexts, no call types have ever been found to be context-specific (Ford, 1989).

Each of the resident killer whale pods off British Columbia has its own stable and unique acoustic repertoire consisting of 7-17 discrete calls (Ford, 1989). These calls differ between matrilines within pods (Ford, 1991; Deecke et al, 2000; Miller & Bain, 2000), with smaller differences between individuals within the same matriline (Nousek et al, 2006). Information on the sex of a caller appears to be present in the relative level of harmonics, which is likely the result of differences in body size (Miller et al., 2007). Ford (1991) suggested that all pods that share at least one call type can be grouped into an acoustic clan. It has been suggested that call repertoires provide information on group identity and help maintain group cohesion when members are separated (Ford, 1991; Filatova et al., 2011). The fact that killer whales mate with conspecifics from different pods or clans suggests they may use calls as a means to assess group membership of potential mates in a reproductive context (Barrett-Lennard, 2000). Groups of killer whales with no overlap in their discrete call repertoires do, however, share stereotyped whistles, suggesting that whistles may facilitate association between these groups (Riesch et al., 2006).

Discrete calls can be composed of a single component (monophonic) or two simultaneous, independently-modulated, time-frequency contours (two-component or biphonic calls) (Ford, 1987). Because biphonic calls have mixed levels of directionality in the different components, they may provide information on the signaller's direction of movement (Miller, 2002) and may also serve as cohesion signals between members of a pod when several pods are in an area (Filatova et al., 2009). Furthermore, biphonic calls have higher source levels than monophonic calls, and are classified as "long-range" signals, whereas monophonic calls are considered to be "short-range" signals (Miller, 2006).

Changes in the characteristics of the environment may affect the signals used by killer whales. For example, whales change the duration of their calls (Foote et al.,

2004; Wieland et al., 2010), as well as their intensity (Holt et al., 2009), with increasing background noise due to boat traffic. They may also change the frequency modulation of their signals depending upon local conditions. For example, for a short time period, leopard seals and killer whales occur in the same area in Antarctica. However, leopard seals produce signals in the same frequency band as killer whales and consequently when the two species co-occur killer whales appear to shift signal frequency modulation to exploit an unoccupied 'acoustic niche' (Mossbridge & Thomas, 1999).

The vocal behaviour of killer whales appears to be strongly influenced by their prey type (Morton, 1990; Barrett-Lennard et al., 1996; Deecke et al., 2005). For example, killer whales that feed on salmon (*Oncorhynchus* spp.) in British Columbia are vocally active during most behavioural contexts, whereas mammal-eating killer whales primarily produce sounds after a kill (Barrett-Lennard et al., 1996; Deecke et al., 2005). Silent foraging by mammal-eating killer whales has most likely evolved to avoid detection and consequent escape by their marine mammal prey (Deecke et al., 2002). Salmon, on the other hand, have poor hearing sensitivity at the frequencies of killer whale sounds and are therefore less likely to detect the whales and escape (Barrett-Lennard et al., 1996; Deecke et al., 2005).

In Norway and Iceland, fish-eating killer whales also seem to have discrete call repertoires that differ between social groups (Moore et al., 1988; Strager 1993, 1995). Killer whales in Norway produce compound calls, i.e. calls composed of combinations of more than one discrete call. These calls may add size and flexibility to the animals' vocal repertoire, although their exact function is not known (Strager 1993, 1995). It is possible that Icelandic killer whales also produce compound calls but less is known about their vocal repertoire. Calling occurs most often during group feeding in both locations (Simon et al., 2007), which has lead to suggestions that calls are used to coordinate group movements (Similä & Ugarte, 1993; van Opzeeland et al., 2005). Calling during feeding may also function to attract other killer whales to join large carousel feeding groups (Shapiro, 2008). However, calls are also produced during other contexts and so their function is not completely understood. In Iceland a context-specific call type, the 'herding' call, has been described (Simon et al., 2006). The herding call is a distinctive low-frequency and long call that is heard just before a tailslap and is thought to be used to herd the herring before a tailslap (Simon et al., 2006).

Most studies on the acoustic behaviour of North Atlantic killer whales have been carried out in Norway and Iceland, however very little is known about killer whales in those areas, particularly in comparison to studies conducted in the North Pacific. It is clear from the little that is known that these whales have quite different acoustic repertoires, as indicated by the production of a prey-manipulation signal, the herding-call, and compound calls. The differences in behaviour have even led some authors to suggest that these whales should form a separate ecotype, the Scandinavian herring-eating killer whales (Simon et al., 2007).

Thesis overview

This study attempts to contribute to the knowledge of herring-eating killer whale communication by investigating design characteristics of signals and contextual sound production to try to elucidate the functions of these signals. The specific goals of this thesis are to more fully characterize the sound repertoire of herring-eating killer whales, to describe some fundamental characteristics of the sounds produced by them, and to identify the context in which sounds are produced in terms of underwater depth, diving behaviour, and horizontal movement patterns. The results of these different studies are interpreted in light of the proposed functions of acoustic signalling by herring-eating killer whales.

Killer whales have been thought to produce whistles with fundamental frequencies limited to the audible frequency range (Thomsen et al., 2001). However, most studies on whistle repertoires to date have focused on killer whales in British Columbia. In Chapter 2, I describe newly-discovered high frequency whistles with fundamental frequencies between 17 and 75 kHz produced by killer whales in the Northeast Atlantic. I compare high sampling-rate recordings of killer whales from three separate locations in the Northeast Atlantic with recordings of resident and transient killer whales from the Northeast Pacific to show that not all killer whale populations produce these signals. I then compare the high frequency whistle repertoires recorded in different locations and discuss possible functions of these signals.

In Chapter 3, I estimate the source levels and active space of burst-pulse calls, herding calls and high frequency whistles produced by killer whales in Iceland. Based on the estimates of active space obtained I discuss possible functions of these signals, in light of what is known from other populations.

Although the diving behaviour of various cetaceans has been studied in detail, little is known about the depths at which animals produce sounds. In Chapter 4, I investigate the depth of sound production and effects of depth on sounds produced by killer whales in Iceland. Finally in Chapter 5 I use sound and movement recording Dtags attached to killer whales in Iceland to investigate the association between sound production and behaviour.

Appendix 1 is a published manuscript that includes part of the results presented in Chapter 2, while Appendix 2 includes additional data plots that are referenced to in Chapter 2 of this dissertation.

Chapter 2

High frequency whistles produced by killer whales (*Orcinus orca*) and their variation across populations[1]

Introduction

The characteristics of a biological signal are shaped by its function and the environmental context it is produced in, as well as the sound production characteristics of the signaller and hearing characteristics of the receiver (Bradbury & Vehrencamp, 1998). Evolutionary studies of acoustic communication based on descriptions of species' signal repertoires seek to identify the selective pressures that influence signal design and variation.

Most odontocete species (Order Cetacea: Suborder Odontoceti) produce tonal signals commonly referred to as "whistles" (see review in Richardson et al., 1995). Comparative studies of whistles produced by odontocetes have shown that there is more variation in whistle frequency parameters among species than within species. Interspecific variation in whistle frequency correlates with phylogenetic relationships (Steiner, 1981; Ding et al., 1995; Matthews et al., 1999; Rendell et al., 1999), environmental characteristics (Ding et al., 1995), selective pressures against hybridization (Steiner, 1981; Rendell et al., 1999), group size (May-Collado et al., 2007a) and body size (Ding et al., 1995; Matthews et al., 1999; Podos et al., 2002). Body size, in particular, correlates negatively with maximum whistle frequency, suggesting that the larger the body size the lower the maximum whistle frequency produced (Ding et al., 1995; Matthews et al., 1999; Podos et al., 2002). However, once phylogeny is taken into account, this relationship no longer holds, and whistle maximum frequency does not seem to be constrained by body size, although the minimum frequency appears to be (May-Collado et al., 2007b). Establishing the factors behind observed variations in odontocete whistles is made difficult by the disagreements between scientists on how to define a whistle (see May-Collado &

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[1] Part of the results presented in this chapter were published in the Journal of the Acoustical Society of America (see Appendix 1)

Wartzok, 2007). Furthermore, the lack of recordings from a number of species makes it difficult to draw conclusions from comparative studies on the origin and evolution of whistles.

Measurements describing acoustic signals are inherently constrained by acoustic sampling decisions. For example, the location of the acoustic receiver relative to the signalling animal will affect the ability to detect low intensity, high frequency or highly directional signals (Miller, 2002, 2006). Furthermore, an insufficient sampling frequency may result in entire signals, or parts of them, being missed (e.g., Oswald et al., 2004). Conventional recording equipment generally has had a maximum sampling frequency of 48 kHz, which, according to Nyquist's law, limits analysis bandwidth to 24 kHz. Until recently there were few inexpensive, broadband options for field recording equipment (Au et al., 1999). Consequently, most studies on odontocete whistles have recorded the frequency range audible to humans (up to 20 kHz) using hydrophones deployed tens to hundreds of meters from signalling animals. Although these hydrophones may be able to capture a significant portion of a species' whistle repertoire, any whistles that extend beyond those frequencies will be missed. Recent studies using broadband recording equipment have shown that several species produce whistles extending well into the ultrasonic range [e.g., bottlenose dolphins (*Tursiops truncatus*, up to 41 kHz; Boisseau, 2005), white-beaked dolphins (*Lagenorhynchus albirostris*, up to 35 kHz; Rasmussen & Miller, 2002), Guyana dolphins (*Sotalia guianensis*, up to 48.4 kHz; May-Collado & Wartzok, 2009), boto (*Inia geoffrensis geoffrensis,* up to 48.1 kHz; May-Collado & Wartzok, 2007)].

Whistles are an important part of the signal repertoire of many odontocetes and are proposed to function in social contexts (e.g., Cook et al., 2004; Rasmussen & Miller, 2002) and, in some cases, in feeding (e.g., Acevedo-Gutiérrez & Stienessen, 2004; Herzing, 1996). However, in the boto whistles seem to be used for keeping distance instead of cohesion between individuals (May-Collado & Wartzok, 2007). Some species produce signature whistles, with a unique frequency-modulated contour that is hypothesized to encode individual signaller identity. Signature whistles were first identified and described in bottlenose dolphins (Caldwell & Caldwell, 1965; Tyack, 1986a; Caldwell et al, 1990; Sayigh et al., 1990; Janik et al., 1994; but see McCowan & Reiss, 1995, 2001 for a divergent view). These signals appear to function in maintaining cohesion during isolation (Janik & Slater, 1998) and socializing contexts (Cook et al., 2004), and in mediating mother-calf reunions

(Smolker et al., 1993). Signature whistles have also been found in other species, suggesting their occurrence may be common in odontocetes [e.g., common dolphin (*Delphinus delphis*): Caldwell & Caldwell, 1968; narwhal (*Monodon monoceros*): Shapiro, 2006; Pacific humpback dolphins (*Sousa chinensis*): Van Parijs & Corkeron, 2001; Pacific whitesided dolphins (*Lagenorhynchus obliquidens*): Caldwell & Caldwell, 1971].

Acoustic signals produced by terrestrial mammals may contain information on individual identity in the resonance patterns generated by effects of filtering in the vocal tract ('voice' cues; e.g., Rendall et al., 1998). Each individual's supralaryngeal vocal tract has a specific size and shape that may give rise to distinctive filtering effects. Unlike voice cues in terrestrial animals, information on individual identity is encoded in the frequency contour of signature whistles (Janik et al., 2006). This signal design feature is thought to arise due to environmental constraints. As diving animals are subject to different pressures, compression of gas-filled vocal tract structures, changing their shape and size, would make voice cues unreliable (Tyack, 1997; Tyack & Miller, 2002). Information on individual identity is relevant in a social system based on strong individual-specific relationships (Tyack, 1986b), such as the fission-fusion social system of many delphinid species (e.g., Smolker et al., 1992).

Killer whales (*Orcinus orca*) are known to produce whistles although, in contrast to other delphinids, they are not the most common vocalization produced (Ford, 1989; Strager, 1995). Killer whale whistles are generally more complex and longer than other delphinid whistles (Thomsen et al., 2001), and are mostly used during social interactions, where they appear to play a role in short-range communication (Ford, 1989; Thomsen et al., 2002; Saulitis et al., 2005; Simon et al., 2007). The estimated active space of a sample of whistles recorded from northern resident killer whales in British Columbia was calculated to be less than that of calls recorded from the same groups (Miller, 2006). In addition, Icelandic and Northwest Atlantic killer whales produce whistles during coordinated feeding behaviours (Steiner et al., 1979; Simon et al., 2007). Whistles produced by fish-eating killer whales in British Columbia are produced in complex sequences and have stereotyped frequency contours (Riesch et al., 2006, 2008). However, these stereotyped whistles are not unique to individuals but are shared among groups that otherwise have different communication signal repertoires. They may, therefore, facilitate associations between these groups (Riesch et al., 2006). Killer whales live in stable matrilineal groups with no dispersal of either

sex, and related matrilines often associate to form pods (Bigg et al., 1990). The stability of these groups may explain why group, rather than individual, identity information is encoded in the frequency contour of killer whale communication signals (Tyack, 1986b).

Killer whales are the largest delphinid and are therefore a particularly interesting species in which to investigate the relationship between body size and whistle frequency. Although the harmonics of killer whale calls and whistles can extend well above 20 kHz (e.g., Miller, 2002), their fundamental frequencies have only been reported up to 16.7 kHz (Thomsen et al., 2001). Importantly however, most studies of killer whale whistle production have investigated the frequency band audible to humans (up to 20 kHz). Here, I use high sampling rate recordings from populations of killer whales in the Northeast Atlantic and the Northwest Pacific to demonstrate that, in certain populations, their whistles extend to ultrasonic frequencies (> 20 kHz). In those populations that do produce high frequency whistles, I investigate the variation in the high frequency whistle repertoire and, in light of this, discuss possible functions of these signals.

Methods

Data collection

Acoustic recordings were collected off British Columbia, Alaska, Norway, Iceland and the UK (Shetland) using a 96 kHz sampling rate (Table 2.1). Recordings off British Columbia were collected and kindly provided by Patrick Miller. Additional recordings off British Columbia, Alaska and Shetland were collected and kindly provided by Volker Deecke. Recordings off Iceland collected in 2004 were kindly provided by Claire Lacey as part of the International Fund for Animal Welfare/The Song of the Whale Team. Only fish-eating Northern Residents (Ford et al., 1998) were recorded in British Columbia and only mammal-eating West Coast Transients (Ford et al., 1998) were recorded in Alaska. No effort was made to control the orientation or range of the whales to the recording devices, and no consistent notes on behaviour or group identification of recorded whales were available. Nevertheless, given that the sample from each location included recordings from multiple days and years (Table 2.1) it is likely that each sample covers several different groups and behaviours.

Recording systems varied between locations; they included towed and vertical hydrophone arrays and sound recording tags attached to whales using suction cups ("Dtags"; flat frequency response 0.6-45 kHz and aliasing avoided using sigma-delta conversion, with -3 dB points at 48 kHz for 96 kHz sampling rate and 67 kHz for 192 kHz sampling rate; Johnson & Tyack, 2003; Madsen et al., 2005). The following towed array recording systems were used: a 16-element array (Miller & Tyack, 1998) recording onto a Pioneer© D-9601 (frequency response 0.020-44 kHz, ±0.5 dB), and re-digitized at a 96 kHz sampling rate using an Edirol© FA-101 soundcard (frequency response 0.02-40 kHz, +0/-2 dB) and recording onto a laptop using Adobe Audition; a 16-element array (Miller & Tyack, 1998) recording onto an Alesis© ADAT-HD24 XR (frequency response 0.022-44 kHz, ±0.5 dB); a 2 element (Benthos© AQ-4; frequency response 0.01-40 kHz, ±3 dB) array connected to a M-Audio© 66 soundcard (frequency response 0.022-40 kHz, ±0.3 dB) and recording onto a laptop; and a 2 element (Benthos© AQ-4 with Magrec© HP-02 pre-amplifiers; frequency response 0.1-40 kHz, ±3 dB) array recording onto a Marantz© PMD671 (frequency response 0.02-44 kHz, ±0.5 dB). The vertical array consisted of four elements (High Tech Inc© 94-SSQ with pre-amplifiers; flat frequency response 0.002-30 kHz) connected to an Edirol© FA-101 soundcard (frequency response 0.02-40 kHz, +0/-2 dB) and recording onto a laptop using PAMGUARD (Gillespie et al., 2008). Not all recording systems were reported to have a flat frequency response up to 48 kHz, but all systems were capable of detecting acoustic energy up to this frequency. Care was taken not to make measurements in frequency bands affected by reduced receiver sensitivity or close to the Nyquist frequency if aliasing seemed to be occurring.

A smaller sample of higher-frequency recordings was collected in Norway and Iceland using Dtags attached to killer whales and using the vertical hydrophone array sampling at 192 kHz (Table 2.1). Additionally, recordings kindly provided by Marianne Rasmussen and Katja Vinding were collected in Iceland in 2008 using a Bruel and Kjær© 8101 single hydrophone (flat frequency response 0.001-120 kHz) connected to an Etec© amplifier and recorded on a laptop using a National Instuments© (DACQ) board (USB 6251; frequency response: 0.001-500 kHz, ±0.5 dB) sampling at 500 kHz (Table 2.1).

Acoustic analysis

High frequency whistles were defined as tonal sounds with fundamental frequency contours entirely above 17 kHz, as this was the maximum frequency previously reported for killer whale whistles (Thomsen et al., 2001). Terminology used to refer to tonal sounds of short duration varies between authors. For example, Bazúa-Durán & Au (2002) refer to whistles of less than 300 ms as 'chirps', although they recognise that this distinction is arbitrary. Other authors use the term 'whistle' to describe bottlenose dolphin signature whistles as short as 100 ms (Buckstaff, 2004), white-beaked dolphin whistles as short as 30 ms (Rasmussen & Miller, 2002) and boto whistles as short as 2 ms (May-Collado & Wartzok, 2007). Given the current lack of knowledge on the potential functions of whistles of different durations, no distinction between whistles based upon duration was made here. Recordings were inspected using Adobe Audition 2.0© (Blackmann-Harris window; FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; 100% window width) and the beginning and end time of each detected high frequency whistle were marked.

Whistle contours entirely above 17 kHz and with sufficient signal to noise ratio were traced from visual inspection of the spectrogram using a peaks contour extraction algorithm (Buck & Tyack, 1993; Hann window; frequency resolution=46.875 Hz; time resolution=0.667 ms). The following descriptive parameters were measured from the extracted fundamental frequency contour: beginning, half-way point (mid) and end frequency, minimum and maximum frequency, frequency range (maximum-minimum frequency) and duration. No contours were extracted from the 500 kHz sampling rate single hydrophone recordings made in Iceland because these recordings were made at the same time as vertical array recordings, thus extracted contours would likely be duplicates. Nevertheless the systems' wide frequency bandwidth allowed the investigation of whistle harmonics, although only a descriptive analysis could be made because it was not possible to control for range or orientation of whales.

Table 2.1 Summary of recordings analyzed. Recordings were conducted using Towed Array (T.A.), Vertical array (V.A.) or Dtags. Recordings made during one day were usually of the same group, therefore number of days was used as a proxy for number of encounters. The recordings obtained in Iceland in 2004 were collected off the Reykjanes peninsula, while the remaining recordings from Iceland were obtained off Vestmannaeyjar. Adapted from Samarra et al. (2010).

Location	Year	Recording method	Sampling rate (kHz)	No. of encounters	Recording duration (h:min)	Total high frequency whistles recorded	% contours extracted
British Columbia	1998	T.A.	96	23	46:55	0	0 %
	2009	Dtag	96	12	57:49	0	0 %
Alaska	2006	Dtag	96	9	79:20	0	0 %
	2007	Dtag	96	2	21:00	0	0 %
Norway (Vestfjord)	2005	T.A. and Dtag	96	13	28:26	134	53 %
	2006	T.A. and Dtag	96	5	12:46	94	45 %
	2007	T.A.	96	5	13:39	55	36 %
	2008	T.A.	96	1	04:37	9	78 %
	2008	Dtag	192	1	15:43	36	61 %
	2009	Dtag	192	1	11:52	58	31 %
	2009	Dtag	96	1	13:21	236	33 %
Iceland (Reykjanes and Vestmannaeyjar)	2004	T.A.	96	2	00:42	62	60 %
	2008	V.A.	96	7	16:07	436	50 %
	2008	Single hydrophone	500	3	11:32	78	0 %
	2009	Dtag	192	3	12:17	403	40 %
	2009	Dtag	96	1	04:12	100	43 %
	2009	V.A.	192	12	30:39	864	13 %
Shetland	2009	T.A.	96	1	00:28	11	73 %

High frequency whistle variation

Intraspecific variation in acoustic signals can be investigated by comparing sound repertoires, using methods based on classification of sounds, or by comparing the parameters of sounds, using methods that do not require classification. Classification based approaches assume that signals can be divided into discrete types and that these divisions are biologically relevant. Non-classification based approaches compare signal parameter measurements, which makes analysis easier to replicate and avoids the potential biases of classification performed by human observers. Both approaches have pitfalls, and the performance of each may vary according to the data available (e.g., Janik, 1999; Rendell & Whitehead, 2003). Using a combination of classification and non-classification based approaches should allow for a comparison of methods as well as provide the most complete analysis. Here, I used two non-classification based and two classification based methods to investigate the patterns of variation in high frequency killer whale whistles.

Non-classification based approaches

A comparison of high frequency whistles produced by different populations was first conducted by testing for differences in whistle contour parameters. The distributions of all whistle parameters were inspected and tested for normality using Wilk-Shapiro tests. Given that all parameters were found to be non-normal (see Appendix 2), non-parametric Kolmogorov-Smirnov tests were used. A Bonferroni correction was applied to the significance level to take account of the multiple comparisons. Whistle parameters were then input into a multivariate discriminant function analysis to classify whistles from different populations. All statistical analyses were conducted in R 2.11.1 for Mac OS.

Classification based approaches

The comparison of whistle parameters does not provide any information on the differences in whistle type usage within each population and may be a coarse way of comparing repertoires. Therefore, whistles were categorized using two approaches: automated categorization and visual categorization by human observers. Automated categorization was conducted by inputting all extracted fundamental frequency contours into an adaptive resonance theory neural network (see Deecke & Janik, 2006 for details) in MATLAB (version 7.0.4). This method compares the similarity of input

and reference contours to a predetermined threshold, called the vigilance parameter, to decide how each input contour should be classified. To find the categorization that would explain most variation in high frequency whistles with the least number of categories, the vigilance parameter was set to values between 0% and 100% in 50 logarithmic steps, and all contours were categorized for each vigilance parameter value. The optimal categorization should have the highest variance ratio, calculated as the ratio of average within-category similarity over average between-category similarity as in Deecke & Janik (2006). The time resolution of each contour was changed from 0.6 ms to 2 ms, the smallest resolution that ensured a reasonable analysis timeframe. The generated categories were inspected visually to verify the categorization results. To evaluate the performance of the categorization, generated categories were inspected to see if whistles with no inflection points were included in the same category as whistles with at least one inflection point. This criterion was chosen because many classification schemes use inflection points to distinguish between whistle types.

Visual categorization was conducted by one observer (Samarra) who compared the entire sample of high frequency whistles (n=835) using spectrograms of each whistle generated in MATLAB (version 7.0.4; spectrogram parameters: FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; overlap=87.5%; window function=Hann; frequency resolution=46.9 Hz; time resolution=2.67 ms). The observer was blind to the origin of high frequency whistles (Iceland, Norway or Shetland). A preliminary analysis suggested that high frequency whistle types were difficult to define. High frequency whistle contours seemed to vary in a continuum, instead of being separated into clear and distinct types. This has also been observed in the whistles produced by other delphinids, which led authors to classify them into broad categories (e.g., Taruski, 1979; Bazúa-Durán & Au, 2002; Azevedo & Van Sluys, 2005). Therefore, high frequency whistles were classified according to their time-frequency contour into six broad categories: upsweeps (rise in frequency with no inflection points), downsweeps (decrease in frequency with no inflection points), ascending-descending (rise in frequency followed by one inflection point and then a decrease in frequency), descending-ascending (decrease in frequency followed by one inflection point and then an increase in frequency), constant (small or no change in frequency and no inflection point), and other. Inflection points are changes in the sign of the slope of the frequency contour (as in Steiner, 1981).

To ensure that this categorization was not too broad and did not overlook real and clearly defined differences between whistle repertoires, five observers with no previous experience in sound classification independently classified 84 (10%) randomly chosen whistles. Untrained observers were chosen because observer experience does not improve classification performance and untrained observers are probably less likely to be biased due to previous experience (Jones et al., 2001). The subsample given to the observers consisted of spectrograms of 84 whistle contours and was representative of the original sample of 835 whistles in that it contained the same proportion of whistles from each location (1% from Shetland, 30% from Norway and 69% from Iceland). The five untrained observers were also naïve to whistle origin. Each observer was asked to classify whistle contours by their shape and group similar contours into as many types as appropriate. No instructions were given as to how similar contours had to be to be considered part of the same category, or how many total categories should be generated. Categories generated by each observer were inspected to see if whistles with no inflection points were included in the same category as whistles with at least one inflection point, as a measure of the performance of classification.

Results

Killer whale whistles were found to extend into the ultrasonic frequency range with observed fundamental frequencies ranging up to 75 kHz (Figure 2.1; Table 2.2), which is higher than previously described for any delphinid. However, high frequency whistles were only detected off Iceland, Norway and Shetland, and not in British Columbia or Alaska. High frequency whistles were detected in most encounters (Iceland=96%; Norway=73%; Shetland=100%; Table 2.1) and occurred during bouts of production of pulse calls. However, they represented on average only 6% (Norway, based on 14 Dtags), 10% (Iceland, based on 4 Dtags) and 2% (Shetland, based on 1 towed array recording) of communicative signals detected (including pulse calls, low and high frequency whistles).

High frequency whistles were short (Table 2.2; Figure 2.1) and most had an entirely ultrasonic (> 20 kHz) fundamental frequency contour (Iceland=97%; Norway=99%; Shetland=87.5%). Some of the whistles detected in the smaller sample from Dtags collected at 192 kHz had a fundamental frequency contour entirely above 48 kHz (Figure 2.1c), but these were usually less frequent than whistles in the 17-48

kHz band. In one Dtag record from Norway 2008, however, only whistles above 48 kHz were detected. Overall, whistle contour frequency parameters showed the lowest coefficients of variation, with the exception of frequency range, and duration showed the highest (Table 2.2).

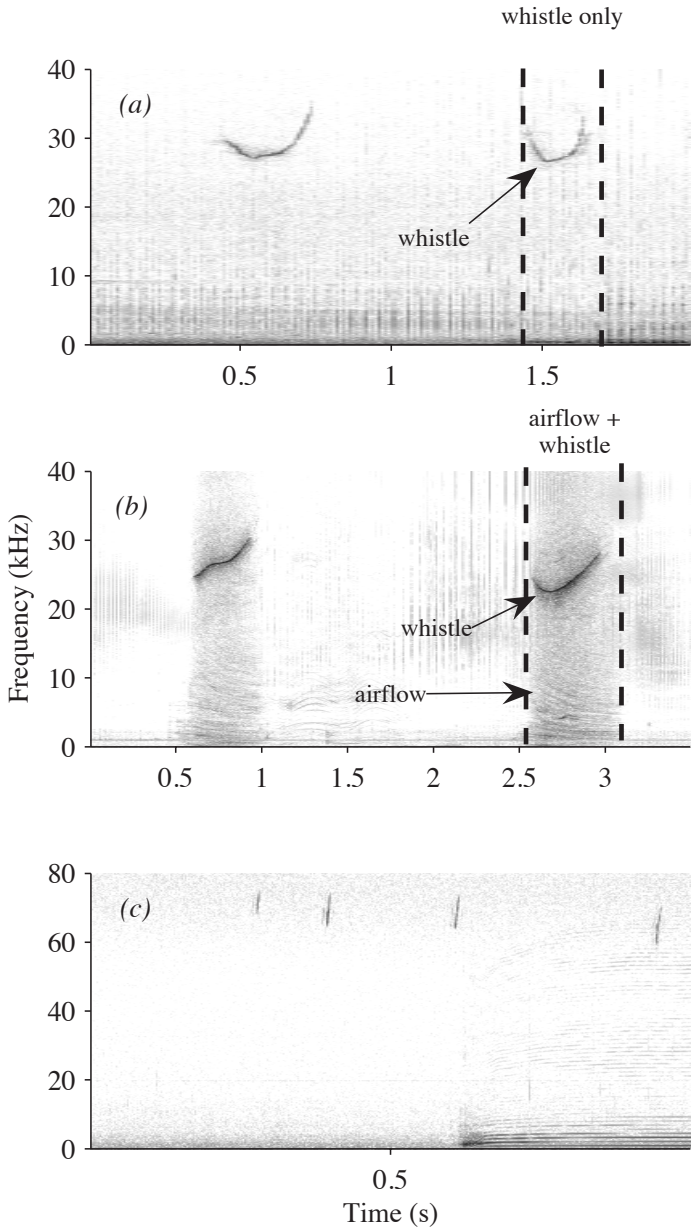

Figure 2.1 Example spectrograms of ultrasonic whistles from Icelandic killer whales (*Orcinus orca*): a) below 48 kHz; b) below 48 kHz with overlapping airflow sound; c) above 48 kHz. Note the presence of an airflow sound entirely overlapping the whistles in (b) but not in (a). In (c) a pulsed call with harmonics can be seen at the end of the spectrogram at lower frequencies. Recordings (a) and (c) were sampled at 192 kHz, and (b) at 96 kHz. Spectrogram parameters: FFT size: (a) 4094, (b) 2048, (c) 1024; overlap: 50%; window function: Hann; frequency resolution: (a) and (b) 46.9 Hz, (c)

187.5 Hz; time resolution: (a) and (b) 10.67 ms, (c) 2.67 ms. Reprinted from Samarra et al. (2010).

No whistles detected with the single hydrophone sampling at 500 kHz had fundamental frequencies above 48 kHz (n=78). Sixty-five of the 78 high frequency whistles detected with this recording system had at least one harmonic. Of these, only 22 had harmonic energy extending above 100 kHz, with 164 kHz being the maximum frequency of any harmonic.

High frequency whistle variation: non-classification based approaches

Given the non-normal distributions of the measured parameters, Kolmogorov-Smirnov tests were used to test for differences in the parameter distributions of both populations. Whistles recorded off Shetland were excluded from the analysis due to the small sample size (Table 2.2). Whistles completely above 48 kHz came from a small dataset of higher sampling frequency recordings, therefore these were not pooled with whistles below 48 kHz. Given the small sample size of whistles completely above 48 kHz from both Norway and Iceland (Table 2.2), only comparisons of the 17-48 kHz whistles were conducted. Due to a strong correlation between beginning and minimum frequency (r_{Iceland}=0.97; $t_{\text{df=546}}$=87.03; p<0.01; r_{Norway}=0.95; $t_{\text{df=232}}$=47.35; p<0.01; Appendix 2) and between end and maximum frequency (r_{Iceland}=0.98; $t_{\text{df=546}}$=129.11; p<0.01; r_{Norway}=0.96; $t_{\text{df=232}}$=52.00; p<0.01; Appendix 2), beginning and end frequency were not compared between populations. Therefore, only five different parameters (minimum, maximum and mid frequency, frequency range and duration) were compared and the significance level was corrected from 0.05 to 0.01.

There was a significant difference in maximum frequency (Kolmogorov-Smirnov test statistic=0.21, p<0.001), frequency range (Kolmogorov-Smirnov test statistic=0.20, p<0.001) and duration (Kolmogorov-Smirnov test statistic=0.14, p=0.003) between high frequency whistles recorded off Iceland and Norway. All other frequency parameters were not significantly different. The distribution of maximum frequency from both populations is strongly bimodal. However, whistles from Iceland have peaks at slightly higher frequencies than whistles from Norway (Figure 2.2). The distribution of frequency ranges from both populations (Figure 2.3) shows that, although the ranges overlap, the frequency range in Norway is generally

lower than in Iceland. Finally, the duration of whistles in Norway is slightly higher than in Iceland (see Figure A2-7 in Appendix 2). Taking into account the entire whistle sample, both at 17-48 kHz and >48 kHz, it is clear that all frequency parameter distributions, except frequency range, from both populations have a distribution with three modes (see Appendix 2). This suggests that high frequency whistles are preferentially produced in certain frequency bands.

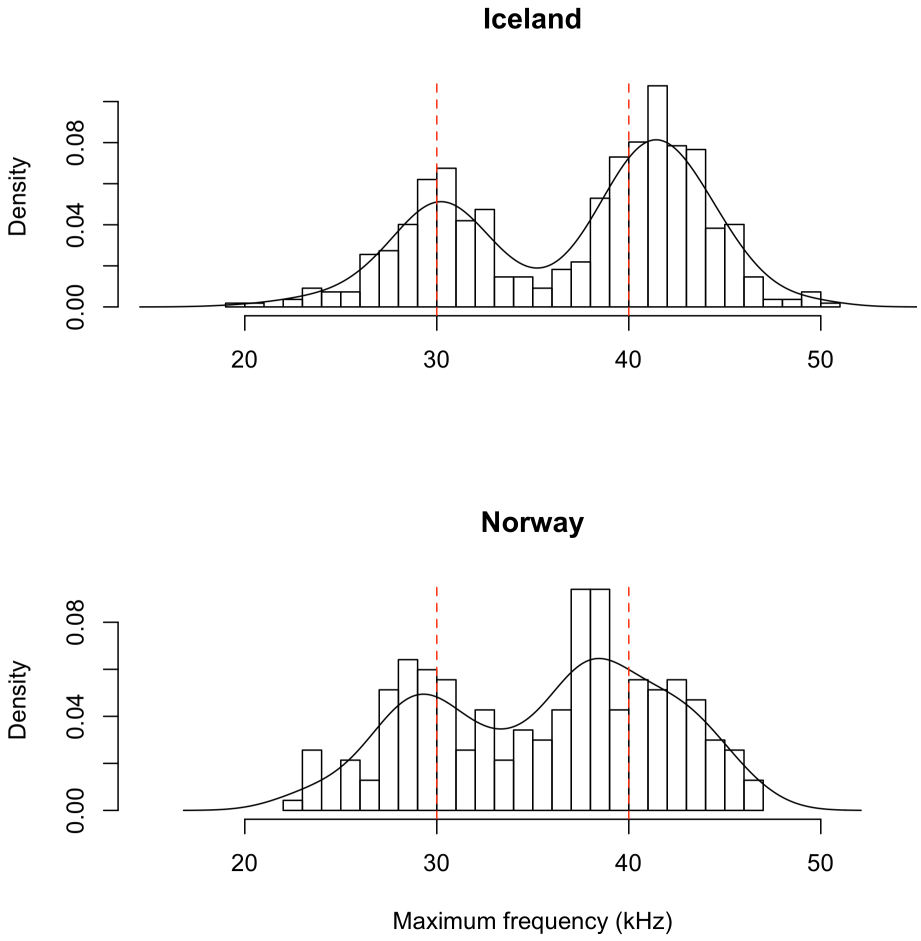

Figure 2.2 Distribution of maximum frequency measured from the fundamental frequency contours of whistles from Iceland (*n*=548) and Norway (*n*=234) with overlapped Kernel density curves (black line). Red dashed lines at 30 and 40 kHz illustrate the difference in frequency of the modes from each population. Note that these distributions do not include whistles with contours entirely above 48 kHz.

Table 2.2 Descriptive statistics of the fundamental frequency contours of high frequency whistles recorded from killer whales off Iceland, Norway and Shetland. For Iceland and Norway, whistles with fundamental frequencies entirely above 48kHz are listed in separate rows. Sample sizes and the Nyquist frequency of recordings from which contours were measured are given in parentheses. Note that descriptive statistics from the Shetland sample may not be representative due to the small sample size. Adapted from Samarra et al. (2010)

	Descriptive statistic	Beginning Frequency (kHz)	Frequency at ½-way point (kHz)	End Frequency (kHz)	Minimum Frequency (kHz)	Maximum Frequency (kHz)	Frequency Range (kHz)	Duration (s)
Iceland (*n*=548, 48 and 96 kHz)	mean ± stdv	31.3 ± 6.7	32.5 ± 5.8	37.0 ± 6.3	30.4 ± 5.9	37.2 ± 6.4	6.8 ± 3.7	0.14 ± 0.14
	range	(16.9-47.3)	(17.6-45.2)	(19.4-50.5)	(16.9-44.5)	(19.4-50.5)	(0.8-21.2)	(0.008-0.81)
	% CV	21%	18%	17%	19%	17%	54%	96%
Norway (*n*=234, 48 and 96 kHz)	mean ± stdv	31.7 ± 6.1	32.1 ± 5.8	35.3 ± 6.4	30.7 ± 5.9	35.7 ± 6.0	5.0 ± 2.5	0.17 ± 0.30
	range	(17.6-45.2)	(19.0-42.8)	(19.8-46.6)	(17.4-42.3)	(22.3-46.6)	(1.0-19.9)	(0.01-4.2)
	% CV	20%	19%	18%	19%	17%	51%	177%
Shetland (*n*=8, 48 kHz)	mean ± stdv	22.6 ± 2.1	23.6 ± 2.7	28.0 ± 3.4	22.2 ± 2.3	28.0 ± 3.4	5.8 ± 2.1	0.34 ± 0.13
	range	(20.2-26.1)	(21.3-29.3)	(25.2-35.3)	(19.9-25.9)	(25.3-35.4)	(3.5-9.5)	(0.14-0.47)
	% CV	9%	12%	12%	10%	12%	36%	37%
Iceland > 48 kHz (*n*=22, 96 kHz)	mean ± stdv	64.0 ± 2.7	65.9 ± 2.3	68.5 ± 3.2	63.1 ± 2.8	68.7 ± 3.0	5.6 ± 2.4	0.04 ± 0.07
	range	(60.6-71.2)	(58.1-68.8)	(60.0-74.7)	(55.6-68.3)	(61.9-74.7)	(0.7-10.4)	(0.006-0.25)
	% CV	4%	4%	5%	4%	4%	44%	184%
Norway > 48 kHz (*n*=23, 96 kHz)	mean ± stdv	64.3 ± 3.6	59.2 ± 3.3	58.1 ± 5.4	55.9 ± 4.0	65.1 ± 3.4	9.1 ± 4.1	0.04 ± 0.03
	range	(56.6-71.0)	(53.3-64.3)	(47.1-68.3)	(47.1-64.3)	(57.9-71.0)	(3.6-19.5)	(0.02-0.14)
	% CV	5%	5%	9%	7%	5%	45%	65%

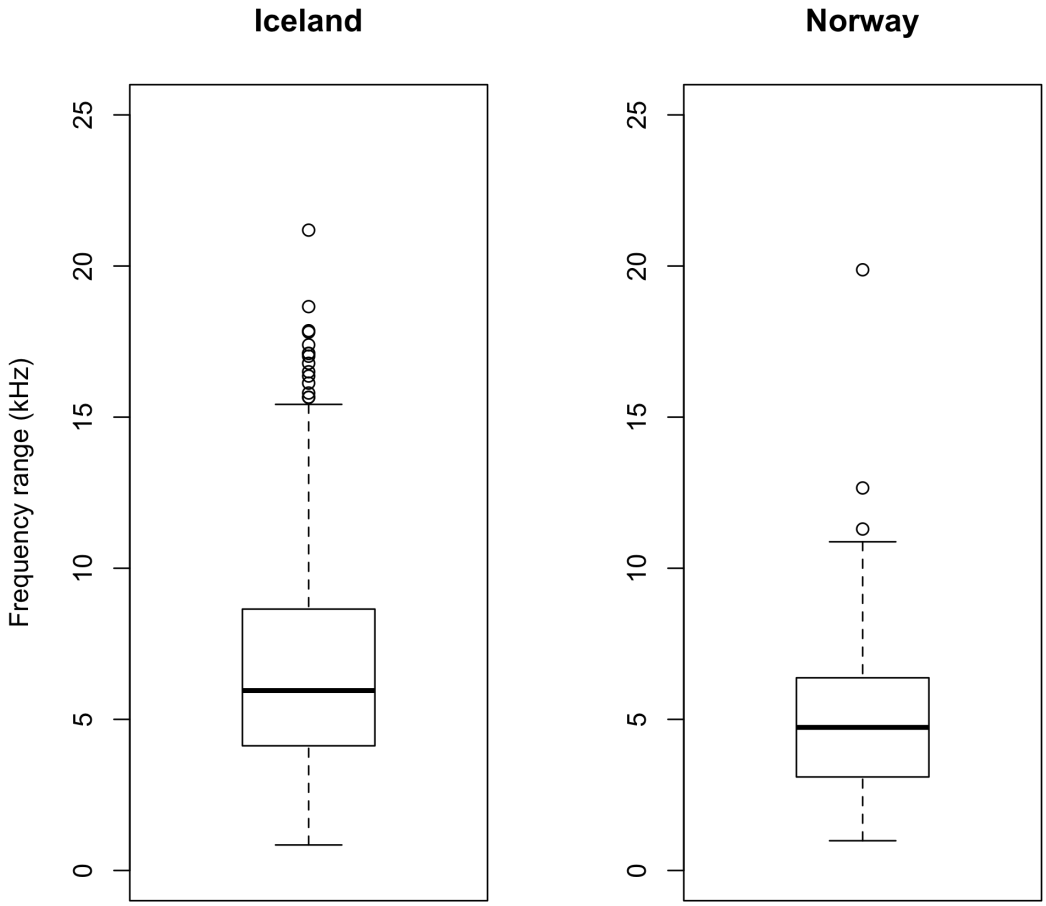

Figure 2.3 Boxplots of frequency range measured from the fundamental frequency contours of whistles from Iceland (n=548) and Norway (n=234). Note that whistles with contours entirely above 48 kHz are not included here.

A discriminant function analysis that included five different parameters to characterise whistle structure (minimum, maximum and mid frequency, frequency range and duration) was conducted using the 17-48 kHz whistles from Iceland and Norway ($n_{Iceland}$=548; n_{Norway}=234). Ninety-nine percent of whistles from Iceland were correctly classified, and only 1% were assigned to Norway. On the other hand, 99% of whistles from Norway were assigned to Iceland and only 1% was correctly assigned to Norway. Although the number of whistles correctly classified was significantly higher than that expected by chance (Normal approximation to the Binomial test: z=11.12; $p<0.001$), the vast majority of these correct classifications were of whistles originating from Iceland. In contrast, all but two of the whistles originating from Norway were incorrectly classified, which indicates that it was not possible to clearly distinguish between the two populations.

High frequency whistle variation: classification based approaches

The results of the automated categorization showed that an increase in the vigilance parameter resulted in an increase in the number of categories generated (Figure 2.4a). On the other hand, the variance ratio levelled off at the point when adding more categories did little to improve the categorization, that is, when most variation was explained by the fewest categories (Figure 2.4 b and c). The variance ratio reached a local maximum when the vigilance parameter was 78.8% and levelled off after that point. With this value for the vigilance parameter, the analysis categorized the 835 high frequency whistles into 19 categories, containing between 1 and 136 contours (mean ± standard deviation of contours in each category: 43.9 ± 42.4). Sixteen of the 18 categories with more than one whistle included high frequency whistles from more than one location. The remaining two categories contained whistles from only one location. All whistles from Shetland were grouped in categories with whistles from Iceland and Norway. These results were still consistent at much higher vigilance parameter values, although the total number of categories generated was much higher. For example, at a vigilance parameter of 99.2%, most categories with more than one high frequency whistle (77 of 143) included whistles coming from more than one location.

All of the 18 categories with more than one whistle included at least one whistle that was incorrectly assigned (9.3 ± 10.0% of contours incorrectly assigned in each category). Although this method successfully classified the signature whistles of bottlenose dolphins and burst-pulse calls of killer whales (Deecke & Janik, 2006), the fact that many of the categories grouped whistles with and without inflection points suggests this method may not be the most appropriate for categorization of high frequency whistles.

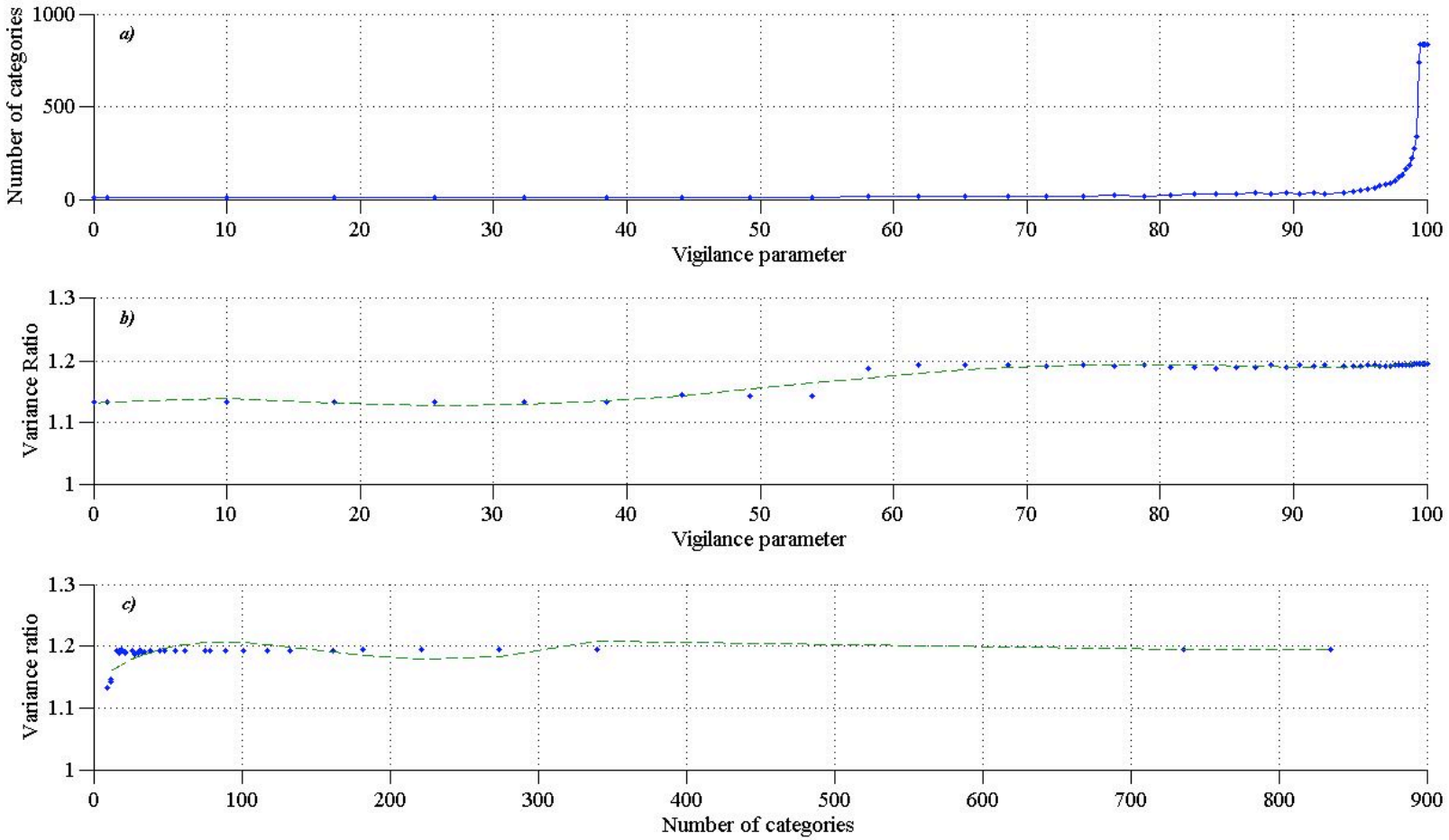

Figure 2.4 Results of categorization of high frequency whistles with different vigilance parameter values: a) total number of categories generated with increasing vigilance; b) change in variance ratio with increasing vigilance (trend line is a sixth-order polynomial); c) change in variance ratio with increasing number of categories (trend line is a sixth-order polynomial).

The visual classification showed that the majority of these signals are very simple (98% have ≤1 inflection points) and most (60%; Table 2.3) are upsweeps. Whistles within each broad category varied only slightly from each other, forming a continuum similar to that described for pilot whale (*Globicephala melas*) whistles by Taruski (1979, Fig. 2). There was a substantial divergence in total number of categories generated by the observers for the same whistle sample (Table 2.4). This could have been due to some observers being 'splitters' while others were 'lumpers', and not necessarily due to disagreement in similarity between whistles. However, the five observers only agreed on the classification of 38% of whistles, and this suggests that the divergence in classification was due to a lack of clear and defined differences between whistles in the sample. The lack of discrete differences between whistles makes their assignment to categories more variable between observers than would be expected if clear categories were present. This inter-observer variation in assignment of whistles to categories was observed in the classification of the random subsample by the five untrained observers.

However, there was a tendency for the untrained observers to group whistles from different locations in the same categories. All but one of the five observers included whistles from different locations in most of their categories, which again suggests similarity of repertoires of different populations. An example of a very similar whistle contour type recorded from Iceland and Norway is seen in Figure 2.5. These whistles were part of the random subset given to the five observers and all observers agreed that they should be included in the same category.

Whistle type use was similar between locations, with upsweeps and descending-ascending whistle types being the most common (Table 2.3). However there were slight differences in the usage of each of these two categories. In Norway, upsweeps and descending-ascending whistles are equally common but in Iceland and Shetland upsweeps are far more common than descending-ascending whistles.

Overall, none of the methods used was able to clearly distinguish whistles from the different locations.

Table 2.3 Proportion of high frequency whistles of each category produced by killer whales in Iceland, Norway and Shetland. Desc-Asc stands for descending-ascending and Asc-Desc stands for ascending-descending whistles.

	Upsweep	**Downsweep**	**Desc-Asc**	**Asc-Desc**	**Constant**	**Other**
Iceland (*n*=570)	68.4%	1.4%	28.6%	0%	0.2%	1.4%
Norway (*n*=257)	41.2%	9.3%	42.8%	0.8%	0%	5.8%
Shetland (*n*=8)	62.5%	0%	37.5%	0%	0%	0%
Total (*n*=835)	60%	3.8%	33.1%	0.2%	0.1%	2.8%

Table 2.4 Summary of categorization of a subset of high frequency whistles (*n*=84) by five untrained observers. The percentage of categories including whistles from more than one location includes only those categories with more than one whistle.

Observer	**Total categories**	**Number categories with only 1 whistle**	**% categories including whistles from more than one location**
Obs. 1	27	11	56%
Obs. 2	11	2	78%
Obs. 3	29	10	47%
Obs. 4	16	2	71%
Obs. 5	17	3	71%

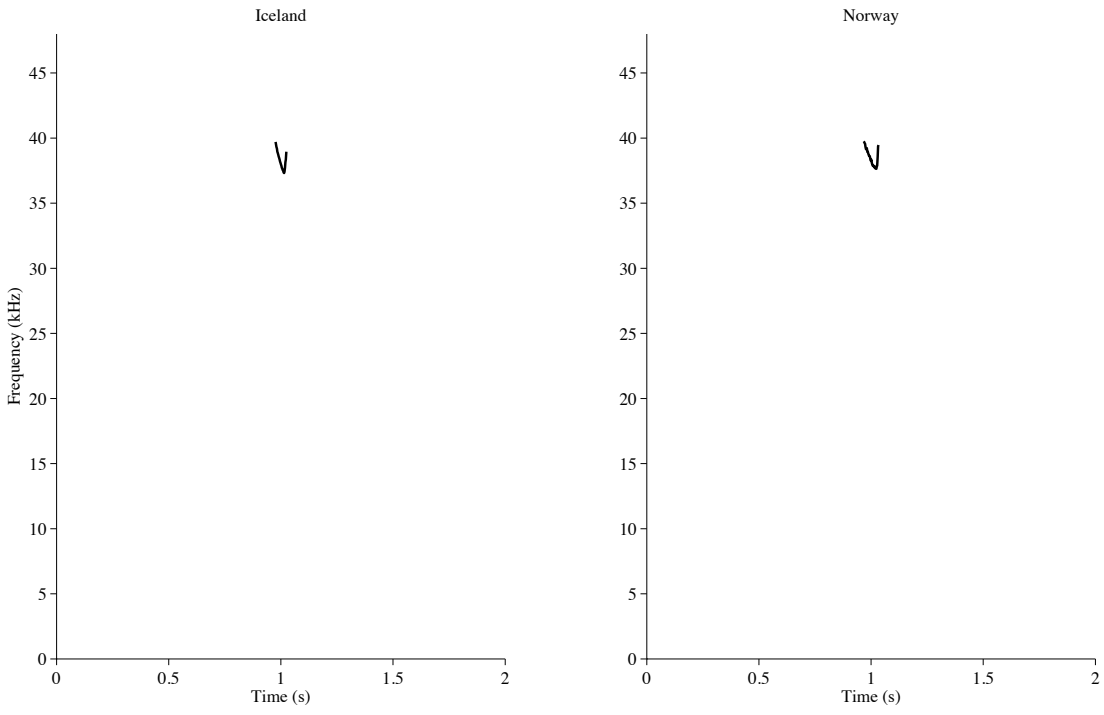

Figure 2.5 Example of high frequency whistle contours from Iceland and Norway. Note the high similarity between both contours despite being recorded in two separate locations.

An example of individual production of high frequency whistles

One of the Dtags was deployed on a large juvenile in Iceland for a total duration of 4.2 hours. Unlike usual deployments, which are close to the dorsal fin, this Dtag was attached close to the blowhole (Figure 2.6).

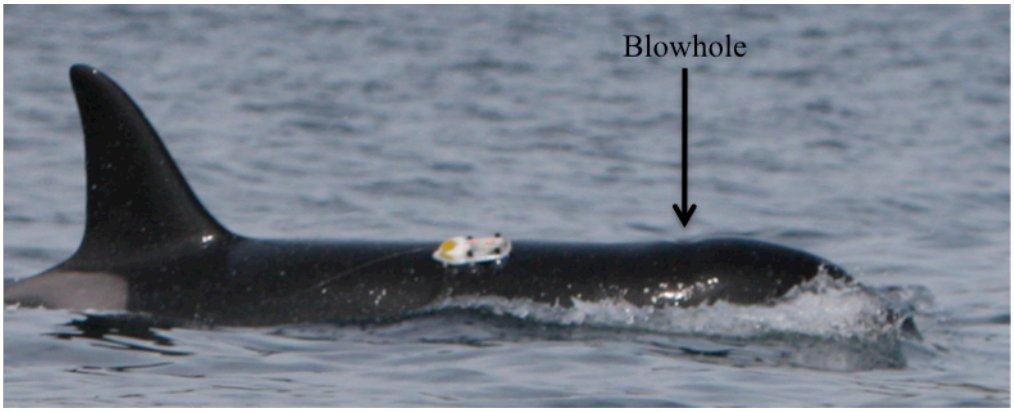

Figure 2.6 Dtag deployed on a large juvenile killer whale in 2009 in Iceland. Note the proximity of the tag to the blowhole. (Photo courtesy of Ralph Baylor)

Air movement sounds clearly overlapped some intense whistles recorded during this Dtag deployment (Figure 2.1b and Figure 2.7). Most of the energy of the airflow sound is in lower frequencies, and its frequency decreases through time. The presence of the airflow sound overlapping with the whistles suggested that the tagged animal produced those whistles. Assuming all the whistles produced by the tagged animal should exhibit the same pattern of presence of an overlapping airflow sound, this feature can be used to investigate individual whistle production. Over a total of 4.2 hours of tag deployment, the tagged animal only produced six whistles, i.e. 0.02 high frequency whistles/min. The first whistle was produced approximately 22 minutes before the remaining five. It was produced during a shallow dive, when the animal was at approximately 2.5 metres depth. This was the 6th of a series of 12 shallow dives between two deeper dives during which some clicks and a few loud calls were heard.

The five remaining whistles were produced in a sequence that lasted 20 seconds. The sequence of five whistles was produced during what appeared to be a foraging dive. During this dive the depth varied between 33.5 and 44 metres. There were no sounds produced during the descent phase of this dive or during the 3 shallow dives that preceded it. Once the whale stopped descending 3 fainter high frequency whistles were detected which were followed 12 seconds later by the 5 whistles of the tagged

whale. Time separation between the tagged whale high frequency whistles ranged from 1.5 to 6.9 seconds and all the whistles had different fundamental frequency contours (Figure 2.7). Clicks and buzzes as well as some calls were heard all throughout this dive.

Discussion

This study demonstrates that killer whale whistles can extend into the ultrasonic range, reaching frequencies of 75 kHz. Detected whistles can confidently be ascribed to killer whales as no other cetaceans were observed during recordings off Iceland, Norway and Shetland. Localisation of high frequency whistles using the vertical array resulted in short ranges, agreeing with visual observations of the location of killer whale groups (Chapter 3). Furthermore, air movement sounds overlapped with some intense whistles recorded by one Dtag deployed close to the blowhole. The proximity of the tag placement to the location of the proposed whistle production mechanism in the nasal system (Dormer, 1979; Ridgway et al., 1980) suggests the airflow sound is a whistle production artefact. The frequency characteristics of the air movement sounds suggest that they are caused by airflow into the nasal air sacs, whose resonant frequencies would change as air is passed during whistle production. The detection of these whistle production artefacts indicates that those whistles were produced by the tagged animal.

Although whistles with contours entirely above 48 kHz were less frequent than other whistles and whistle production seemed to be emphasised at certain frequencies, whistles reaching frequencies above 60 kHz were recorded in both Icelandic and Norwegian populations. Killer whales are the largest delphinid and produce the highest frequency whistles reported for a delphinid. This could be a result of the few studies using high sampling rates for other species. Nevertheless, these results suggest that killer whales fall well outside the proposed relationship between body size and maximum whistle frequency (Ding et al., 1995; Matthews et al., 1999; Podos et al., 2002), and reinforce the conclusion that maximum whistle frequency is not constrained by body size in this species group (May-Collado et al., 2007b).

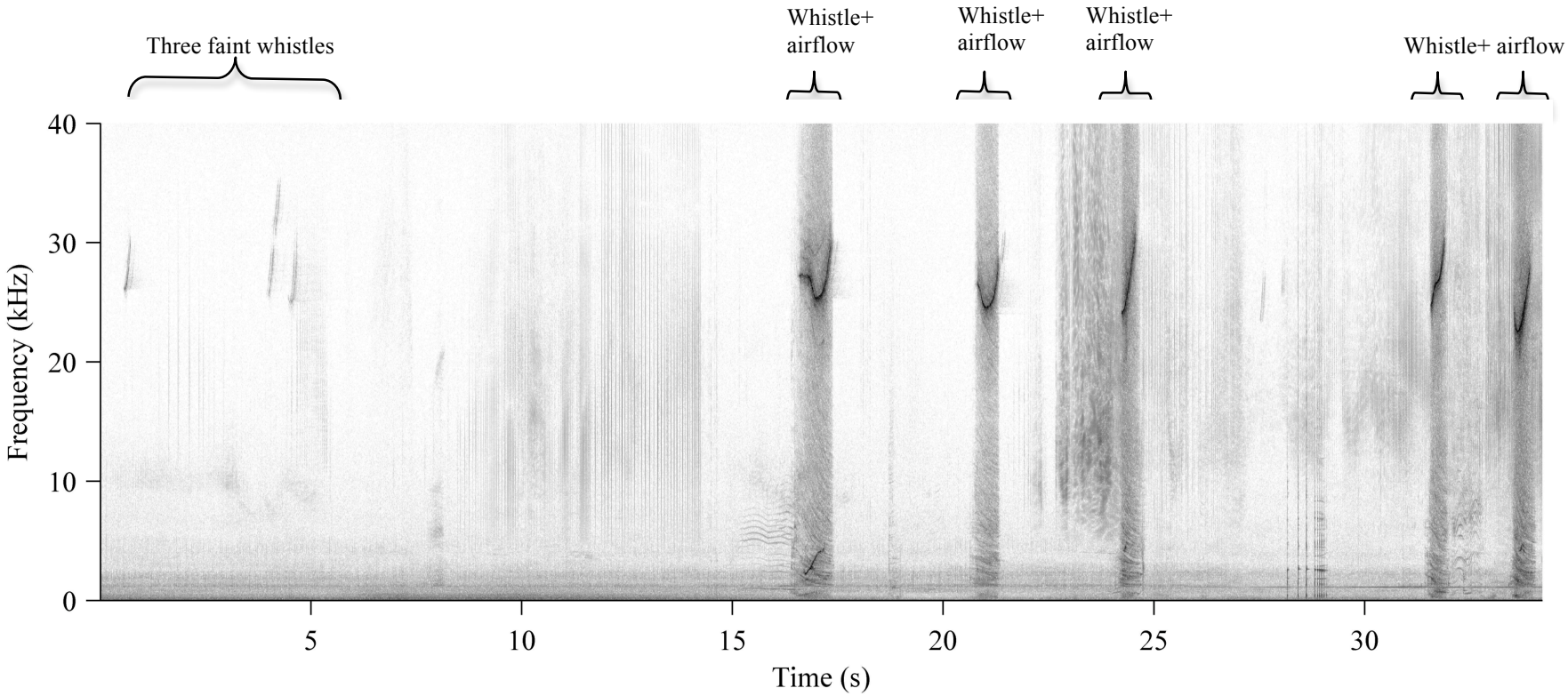

Figure 2.7 Three faint high frequency whistles followed by a high frequency whistle sequence produced by a single individual. Recording made with 96 kHz sampling rate. (Spectrogram parameters: FFT size: 2048; overlap: 50%; window function: Hann; frequency resolution: 46.875 Hz; time resolution: 10.67 ms)

Furthermore, these results indicate the need to use high sampling rates to study the full frequency range of killer whale whistles. Spatial sampling may also play an important role in whistle detection, particularly at these very high frequencies. High frequency whistles with contours entirely above 48 kHz were only detected when using Dtags and not with a single hydrophone deployed from a boat, which was likely further away from the signaller. Although this difference could have been due to chance, it is important not to disregard the effect that higher rates of absorption and directionality of high frequencies can have in our ability to detect sounds. A sampling rate of at least 192 kHz is necessary to fully investigate killer whale whistles. However, a wider bandwidth is necessary to investigate the full energy content of high frequency whistles including the whistle harmonics, which can extend beyond that frequency limit.

Intraspecific variation in whistle production

In contrast to other delphinids, maximum whistle frequency appears to vary substantially between killer whales recorded off the Northeast Pacific and the Northeast Atlantic. Whistles from the ecologically and genetically distinct Northern Residents and West Coast Transients seem to be restricted to the audible frequency range, while whistles recorded off Iceland, Norway and Shetland are commonly produced in the ultrasonic range. Given that in all locations (except Shetland) Dtags were used, which provide the best quality recordings, and the overall sample size from the Northwest Pacific was larger than from the Northeast Atlantic (205 hours vs. 176 hours; Table 2.1), the observed differences between locations do not seem to be due to chance alone. Nevertheless, there were no recordings of Northern Residents or West Coast Transients at sampling rates higher than 96 kHz, which would be necessary to rule-out the possibility that these whales produce whistles entirely above 48 kHz.

Intraspecific variation in signal frequency may result from geographical and social isolation (e.g., Baron et al., 2008) or adaptation to local habitat conditions (e.g., Baron et al., 2008; Rendell et al., 1999). For example, slight variations in the frequency characteristics of killer whale pulsed calls between populations have been found (e.g., Awbrey, 1982; Foote & Nystuen, 2008) and attributed to differences in local ambient noise and potential detection by prey (e.g., Foote & Nystuen, 2008). However, these differences in the maximum frequency of pulsed calls were very

small when compared to the difference in maximum whistle frequency reported here. Icelandic and Norwegian killer whales have been suggested to form a separate ecotype due to their unique behaviour (Simon et al., 2007) and may be under different selective pressures to killer whales in the Northeast Pacific, and this may explain the observed differences in whistle production. Further research is necessary to clarify what factors drive such intraspecific variation in killer whales, nevertheless, these results indicate the importance of sampling different populations to obtain a truly representative sample of the species' whistle frequency parameters for use in comparative studies.

High frequency whistle repertoire comparisons

High frequency whistles produced by killer whales in the three Northeast Atlantic locations were similar both in overall measured parameters and in whistle type repertoire.

None of the methods used was able to consistently distinguish whistles produced in both locations. However, some of the methods used may not have been the most adequate. For example, the automated classification did not seem to classify whistles well, as it grouped whistles with and without inflection points into the same categories. It is possible that decreasing the contour time resolution would have improved the performance of the method, however it was not possible to evaluate that within the time frame of this study. Ultimately, understanding how the animals themselves perceive and use these signals is necessary to decide what particular method is the most appropriate. Nevertheless, all methods suggested some degree of similarity in the high frequency whistle repertoires of Northeast Atlantic killer whale populations.

Killer whales in Iceland and Norway are closely related (Foote et al., 2009a; Morin et al., 2010) and feed on the same prey species, the Atlantic herring *Clupea harengus* (Similä et al., 1996; Sigurjónsson et al. 1988; Simon et al. 2007). Prior to the collapse of the Atlanto-Scandian herring stock in the 1960's, its migration route spanned from Western Norway to Eastern Iceland (Jakobsson & Østvedt, 1999). This led to suggestions that killer whales then might also migrate between Iceland and Norway (Jonsgård & Lyshoel, 1970). The migration patterns of both the Icelandic and Norwegian herring stocks changed following the collapse and remained closer to Iceland and Norway, respectively (Jakobsson & Stefánsson, 1999; Kvamme et al.,

2003). Comparisons of photographs of killer whales taken since the 1980's in Iceland and Norway have found no matches (Sigurjónsson et al., 1988; Foote et al., 2009b), suggesting that even if killer whales migrated between those two locations in the past, they no longer do so.

On the other hand, a more recent analysis of photographs has suggested that there is movement between Iceland and Shetland (Foote et al., 2009b); it is therefore possible that some Northeast Atlantic populations are in contact. Icelandic and Norwegian killer whales have similar acoustic behaviour (Simon et al., 2007) and apparently even share some call types (Strager, 1995; Stenersen & Similä, 2004). Thus, the similarity in high frequency whistle repertoire found here is more likely to be due to contact in the recent past than convergence on the same whistle types. If contact did occur, it is possible that not enough time has elapsed for major repertoire divergence to occur.

The only significant differences between Icelandic and Norwegian killer whales were in frequency range and maximum frequency; Norwegian killer whales also produced proportionately more descending-ascending whistles than did Icelandic and Shetland killer whales. The function of these slight differences is unclear. There were no apparent differences in ambient noise between Iceland and Norway that would justify a shift in maximum frequency, although accurate measurements of ambient noise in both locations would be necessary to confirm this. Similarly, it remains unclear why high frequency whistles appear to be produced more commonly in certain frequency bands in both locations. Nevertheless, all the analyses suggested an overall similarity in high frequency whistle production among Northeast Atlantic killer whales.

This similarity may occur because there was contact in a recent past or because the selective pressures acting upon killer whales in the Northeast Atlantic are similar and lead to convergence in whistle types. For example, similarities in ecology have been suggested as a reason for the similarities in the whistle repertoires of species inhabiting similar habitats (Van Parijs et al., 2000). Furthermore, if the function of high frequency whistles constrains their signal design characteristics, there could have been little selective pressure for signal divergence.

Possible functions of high frequency whistles

Studies in captive killer whales have shown their best hearing sensitivity is between 18 and 42 kHz with an upper hearing limit of roughly 100 kHz (Szymanski et al., 1999). They therefore should be able to detect the whistles described here, although signal duration may affect absolute thresholds (Johnson, 1968). The fact that these signals are recorded in most encounters suggests they are part of their communication system, although it remains unclear how killer whales detect and use high frequency whistles.

The production of tone-like, high frequency sounds by birds and mammals is commonly associated with friendly social circumstances (Morton, 1977). Moreover, ultrasonic signal production in terrestrial vertebrates functions in echolocation, predator avoidance, and short-range social interactions (Arch & Narins, 2008). It can also increase signal-to-noise ratio, by producing signals in a frequency band with comparatively little background noise (Arch & Narins, 2008). In odontocetes, whistles extending into the ultrasonic range are generally used in social contexts (e.g., Rasmussen & Miller, 2002), although they may also be used for keeping distance among animals in botos (*Inia geoffrensis geoffrensis*; May-Collado & Wartzock, 2007). The killer whale high frequency whistles described here are likely associated with short-range social communication. Other functions, such as echolocation or predator avoidance, are unlikely because killer whales use clicks quite extensively for echolocation purposes and they have no known predators. An increase in signal-to-noise ratio is also unlikely because there is no overall shift in sound production towards higher frequencies: Icelandic and Norwegian killer whales also produce lower frequency whistles and burst-pulse calls in addition to high frequency whistles (Strager, 1995; Simon et al., 2007). Furthermore, there was no noticeable change in background noise during the production of high frequency whistles compared to periods without high frequency whistles. On the other hand, the frequency characteristics of high frequency whistles described here mean that they will not propagate far. This suggests that their main use is in short-range communication, as is proposed for lower frequency whistles (Thomsen et al., 2002).

Icelandic and Norwegian killer whales are generally silent when travelling and vocalise most intensively during feeding or socialising (Simon et al., 2007). High frequency whistles are primarily produced during bouts of calling, suggesting that their production is related to such contexts. The presence of harmonics in high

frequency whistles may provide information on the signaller's direction of movement (Miller, 2002; Lammers & Au, 2003). Some delphinids can distinguish between whistles with and without harmonics (Yuen et al., 2007), thus killer whales may be able to use this information, which would be particularly relevant in cooperative contexts.

The complexity of odontocete whistles may vary intra- and interspecifically, and it is unclear whether such variation is simply related to adaptations to local habitat, such as background noise, or the complexity of the information being transmitted (Janik, 2009). Unlike the long and complex low frequency whistles produced by killer whales (Thomsen et al., 2001), high frequency whistles are short and simple; they may therefore encode different information. The fact that the majority of high frequency whistles are upsweeps and there is high similarity between whistle contours from different populations (see Figure 2.4) suggest that these whistles do not encode individual, group or even population information. If whistles were used as group or individual identifiers, as suggested for the lower frequency killer whale whistles (Riesch et al., 2006) and bottlenose dolphin whistles respectively (e.g., Caldwell & Caldwell, 1965), we would expect higher contour variation and complexity. Furthermore, in the Dtag recording that contained the coincident airflow sound, none of the five whistles produced consecutively by the same individual had the same contour. Signature whistles are defined as the most common whistle type produced by an individual in isolation (Caldwell et al., 1990). Consequently, if high frequency whistles were used as a group or individual signature, the tagged individual might be expected to produce one contour type more commonly than the others. Thus, it is unlikely that high frequency whistles serve this function. It is possible that slight variations between individuals producing the same frequency contour type are present, such as in the burst-pulse calls of British Columbia resident killer whales (Nousek et al., 2006). The lack of information on the identity of the individual producing each whistle in the sample used here makes it impossible to test such a hypothesis. However, future studies may show that individual variation exists in this signal.

Non-signature upsweep whistles are an important component of the whistle repertoire of various delphinid species, such as the bottlenose dolphin, both in captivity (Tyack, 1986a; Janik et al., 1994) and the wild (Cook et al, 2004), the Guiana dolphins and tucuxis (Azevedo & Van Sluys, 2005). Such signals do not carry

information on the signaller's identity, as do other whistles in an individual's repertoire. However, they do appear to be a relevant part of the communication system, particularly during socializing, although their specific function is not known (Cook et al., 2004). Similarly, it appears that the high frequency whistles of killer whales reported here are used in short-range social contexts, but not as group or individual identifiers. Future work will be necessary to understand what exact function this novel sound may have and why apparently only Northeast Atlantic killer whales produce it.

Chapter 3

Source levels and estimated active space of burst-pulse calls and high frequency whistles produced by killer whales (*Orcinus orca*) off Iceland

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Introduction

Acoustic signals designed for communication are produced by a signaller and propagate to receivers who can decode the signal and respond to the transmitted information (Bradbury & Vehrencamp, 1998). However, once emitted, a signal deteriorates as it travels trough the environment, because of the effects of scattering, attenuation, absorption, etc. Signal deterioration will vary according to the habitat the sound is produced in, the distance the signal travels, and where it travels through the environment before reaching the receiver (Marten et al., 1977; Marten & Marler, 1977). The receiver will receive the degraded signal and also ambient noise at its location, which may mask the signal and preclude its detection and decoding (Klump, 1996). As signalling ultimately benefits the signaller, the signaller should be selected to emit signals with frequency, amplitude and temporal characteristics increase the probability of it reaching intended receivers with sufficient quality to be decoded.

The source level of a signal is a key characteristic that is predicted to vary according to its function. The source levels of signals within the repertoire of a species may vary according to their functions (Miller, 2006). The more intense a signal is produced, the further it should be detectable by receivers, therefore signals meant for long-distance communication should be produced with higher source levels than those intended for short-range communication. For example, birds shift from a higher amplitude advertising song to lower amplitude high frequency signals for close range communication (Dabelsteen et al., 1998). Zebra finches adjust the song source level according to the distance to the intended receivers (Brumm & Slater, 2006). Characteristics of the environment will also influence the source level with which a signal is produced. For example, signallers may increase the level of emitted signals in the presence of background noise in order to compensate for the increased noise levels in the environment (Lombard effect; Brumm, 2004).

Signal intensity may also provide information about the signaller. For example, in insects (e.g., Gerhardt & Huber, 2002), anurans (e.g., Castellano et al., 2000; Gerhardt & Huber, 2002) and birds (e.g., Searcy, 1996), females tend to approach louder signals, possibly because these are indicators of high-quality males that can support the higher costs of producing such signals (Castellano et al., 2004). Another important cost to signalling may be the increased risk of detection by non-intended receivers such as predators and prey. The balance of benefits and costs should select for signals with the necessary source levels to reach intended receivers at typical ranges.

The maximum range over which a signal can be detected by a conspecific receiver is defined as the signal's active space (Brenowitz, 1982). The active space of any signal is determined by the source level of the signal, the receiver's hearing characteristics, the background noise levels at the receiver's position and the transmission properties of the environment. Cetaceans produce varied acoustic signals and the source levels of sounds studied to date vary between species and according to context (Fish & Turl, 1976; Richardson et al., 1995; Janik, 2009). For example, bottlenose dolphins (*Tursiops truncatus*) produce whistles that can be detected by conspecifics at distances up to 20 km (Janik, 2000b). However, bottlenose dolphin whistle communication ranges will vary with the characteristics of the environment and may be greatly reduced depending on water depth and bottom type (Quintana-Rizzo et al., 2006). Whitebeaked dolphins (*Lagenorhynchus albirostris*) produced higher source level whistles just before other individuals joined their social group suggesting louder signals attracted other conspecifics (Rasmussen et al., 2006). On the other hand, spinner dolphins (*Stenella longirostris*) produced low source level whistles during resting (Watkins & Schevill, 1974), which could have been related to behavioural context.

Killer whales (*Orcinus orca*) produce discrete burst-pulse calls during most behaviours (Ford, 1989). These are thought to act as a group identifier, allowing groups to remain in contact when spread over large distances (Ford, 1991). Calls provide information on group membership, relatedness, and to some level on individual identity and caller sex (Ford, 1991; Deecke et al., 2000; Nousek et al., 2006; Miller et al., 2007). Some call types are composed of two independently modulated frequency contours, a low and a high frequency component, and provide information on signaller orientation, allowing group members to coordinate movements and keep contact when spread over large distances (Miller, 2002; Filatova

et al., 2009). Based upon their estimated active space, these calls appear to function as long-range calls, in contrast to single component calls and whistles that are estimated to have smaller active spaces (Miller, 2006).

In Iceland and Norway, killer whales also appear to have group-specific repertoires of calls (Moore et al., 1988; Strager, 1993, 1995). In addition, killer whales in the North Atlantic produce high-frequency whistles, but their function is unknown (Chapter 2). Killer whales in Iceland and Norway feed mainly on Atlantic herring (*Clupea harengus*) (Sigurjónson et al., 1988; Similä et al., 1996) and increase call production during feeding (Simon et al., 2007). In Iceland, killer whales also produce their only known context-specific call, a low-frequency call produced just before a tail slap called the herding call (Simon et al., 2006). The frequency of the call does not suggest a use in intraspecific communication; instead it is similar to the resonant frequency of the herring swim bladder, suggesting it could be used to manipulate the prey (Simon et al., 2006).

Feeding on schooling prey such as herring generally involves varying levels of coordination between members of a group of whales (Similä & Ugarte, 1993; Similä, 1997; van Opzeeland et al., 2005). Because sound production increases during feeding, particularly production of burst-pulse calls, it has been suggested that calls may be used to help herd the fish or coordinate the groups' movements (Similä & Ugarte, 1993; Simon et al., 2007). In fact, call production is more frequent during carousel feeding, a complex group feeding behaviour, than during other feeding strategies presumably involving less coordinated behaviour (van Opzeeland et al., 2005).

The proposed social functions of calls produced by herring-eating killer whales include attracting other groups to large feeding aggregations, and within-group coordination. These functions have different implications about what communication ranges would be most likely to evolve in signal production. Attracting other groups should favour transmission of high source level signals, while signals with the function of aiding within-group coordination are directed to receivers at short ranges. In this chapter, I provide measurements of the sound pressure levels of burst-pulse calls, including herding calls, and high frequency whistles produced by free-ranging killer whales in Iceland, and estimate the maximum range over which they might be detected by conspecifics. The results are interpreted in relation to the possible functions of these sounds.

Methods

Study area

This study was conducted in Vestmannaeyjar, an archipelago in southwestern Iceland (Figure 3.1). The archipelago is composed of 16 islands and the distance between the furthest islands is approximately 16 nautical miles. This is an area characterized by shallow waters (generally <100 m) and varying bathymetry.

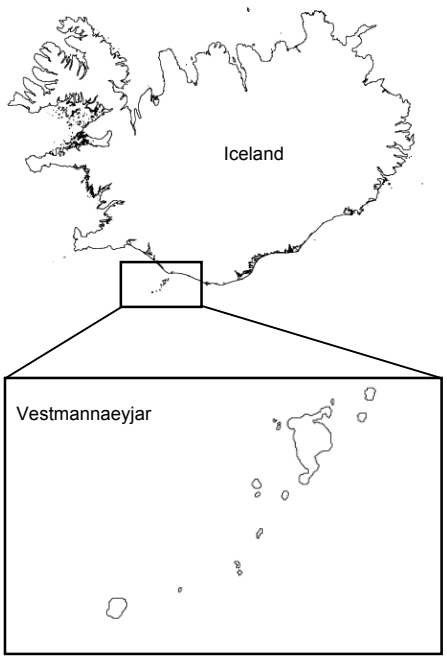

Figure 3.1. Map of Iceland with detail of study area.

Vestmannaeyjar is a spawning ground of the Icelandic summer-spawning (ISS) herring and killer whales are regularly seen in this area feeding on ISS herring in the summer months (Simon et al., 2007, personal observation). Feeding events are generally characterized by whales surfacing in different orientations in a particular area and the presence of pieces of fish or whole fish at the surface. Various species of seabirds are observed during these events, feeding on herring from the surface. Feeding events observed during this study were always presumed to have been directed at herring because when fish were observed at the surface, they were always confirmed to be herring. Although other species of marine mammals (harbour seals *Phoca vitulina*, harbour porpoises *Phocoena phocoena*, minke whales *Balaenoptera*

acutorostrata) are observed in this area, killer whales were never seen interacting with those animals.

Data collection

Acoustic recordings were collected in July 2008 and 2009 using a 4-element vertical hydrophone array (High Tech Inc© 94-SSQ with pre-amplifiers) connected to an Edirol© FA-101 soundcard (frequency response 0.02-40 kHz, +0/-2 dB) and recording onto a laptop as 4-channel wave files using PAMGUARD (Gillespie et al., 2008). Sampling rate was set to 96 kHz in 2008 and 192 kHz in 2009 but all other recording settings were kept the same.

The elements in the hydrophone array had a reported sensitivity of -165 db re 1 V/µPa between 2 Hz and 30 kHz. Although calibrations were conducted to estimate the sensitivity of the hydrophones, results were inconsistent. Therefore, the sensitivity was assumed to be that reported by the manufacturer over the whole frequency band.

Recordings were inspected using Adobe Audition 2.0© (Blackmann-Harris window; FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; 100% window width) and the beginning and end time of each vocalization detected was marked. Each sound was evaluated and assigned a quality based on its signal-to-noise ratio (SNR) as: 1) poor, when a contour was hardly seen in the spectrogram and sometimes only the sound was heard; 2) moderate, when a contour was seen but it was incomplete; and 3) good, when the full contour was clearly seen in the spectrogram. Only sounds of quality 2 and 3 were analysed for localisation.

The hydrophone array was deployed vertically with a spacing of 10 m between elements. The first hydrophone was generally placed at 10 m depth, the second at 20 m depth and so on (Figure 3.2). However water depth was sometimes less than 40 m due to the presence of small seamounts. Therefore, the spacing between elements was adjusted from a default 10 m to whatever spacing was necessary depending on the depth of the water in the area where the whales were encountered. To ensure that the position of each hydrophone was known, a requirement of methods for acoustic localisation, the depth of each hydrophone was continuously monitored using digital dive watches (Suunto D3; sampling depth with an accuracy of ±0.3m every 1s) attached to each hydrophone. A surface float was tied to the top of the array and a 6-8 kg weight tied to the bottom of the hydrophone array to help maintain the array

vertical and avoid wind and currents affecting its geometry (Figure 3.2). The hydrophone array was only deployed in light wind conditions (Beaufort < 3) and once the boat stopped and the engine was switched off.

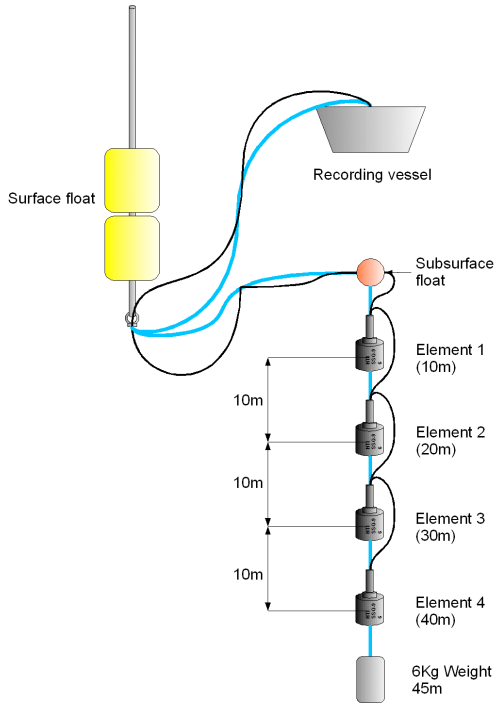

Figure 3.2. Schematic view of the 4-element vertical hydrophone array. Courtesy of René Swift.

The hydrophone depth data were analysed to identify acoustic recordings collected during periods of time when the depths of the hydrophones in the array were stable near the expected depth, i.e., when the average depth of each element did not change. Only recordings conducted during those stable times were analysed. This criterion ensured that times when the array geometry might have been influenced by strong winds or currents were not used.

To further reduce the error from unknown position of the receivers, the precise depth of each element was estimated at the time each localised sound was recorded. However, the dive watches recorded time rounded to the nearest minute, therefore the time of each depth measurement had a 1 min uncertainty (30 s either side of the true time) relative to true time. To compensate for that uncertainty, once a sound was identified and had sufficient quality to be localised, the depth of each receiver at that time was found by taking the average of the depths recorded before and after the time of the localised sound.

Localisation procedure

The position of signalling animals was estimated using custom made software written in MATLAB® (version 7.0.4). The position of the signaller was determined using time-of-arrival differences (TOADs) between the first and each of the remaining hydrophones in the array. The TOADs were measured from the peak of the cross-correlation functions of each hydrophone pair. The cross-correlation function was calculated on a frequency and time section identified by the user by visual inspection of the spectrogram of the first hydrophone of the array. The same section was then cross-correlated with the remaining hydrophones of the array. This allowed the user to select a section of the signal that was not masked by other signals and relatively free of background noise. However, many signals had overlapping echolocation click trains or other killer whale sounds, making it impossible to choose one section for analysis.

The TOADs were used to estimate the source location using the method of Wahlberg et al. (2001). Simultaneously, hyperbola curves were also estimated. Only localisations where the source estimated position was within the point or area resulting from the intersection of the three hyperbolae, i.e. where both methods resulted in the same approximate position, were used (Figure 3.3). I then used the source location estimated with the Wahlberg et al. (2001) method.

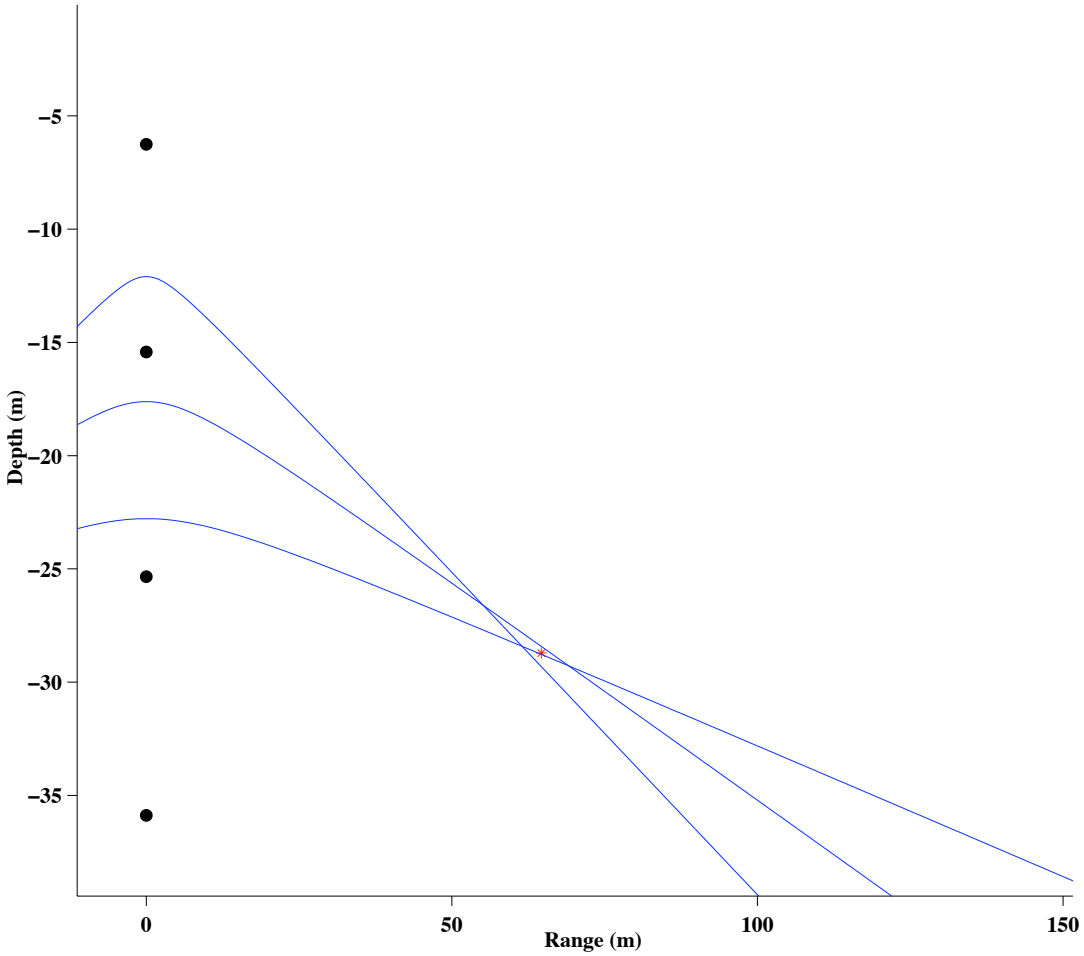

Figure 3.3. Example of a localisation where hyperbolae cross at the same location as the estimated position (red star). Black circles represent the hydrophone locations.

The speed of sound used in the analysis was 1493 $m.s^{-1}$, estimated based on a typical water temperature of 11º C and local salinity of 35.2 ppt. The average temperature and salinity values were taken from hydrographical surveys conducted by the Marine Research Institute in the area in August 2009 (consulted in http://www.hafro.is/Sjora). Average sea surface temperature in Vestmannaeyjar during July and August 1999-2003 was consistent with the value used (Hanna et al., 2006), therefore it seemed reasonable to assume this to be the temperature during the period the acoustic data was collected.

Accuracy of localisation method

A calibration experiment was conducted in order to estimate errors of the localisation method. Killer whale sounds played from a known horizontal distance and depth were localised. The playback system consisted of a Sony D-E201 portable CD player connected to a Cadence Z9000 Stereo amplifier, which was in turn

connected to a Lubell AC203/4 Circuit Master. Sounds were played from a Lubell LL916 underwater speaker. The playback stimulus consisted of a recording of natural sounds produced by killer whales, which included burst-pulse calls, whistles and tailslaps. These recordings had been made using the vertical hydrophone array connected to an Edirol© FA-66 24-bit soundcard (frequency response 0.02-40 kHz, +0/-2 dB) and recording onto a laptop using Adobe Audition 2.0© at a sampling rate of 96 kHz.

The playbacks were conducted in Vestfjord, Norway, where the sound speed was estimated as 1480 $m.s^{-1}$, according to Conductivity-Temperature-Depth (CTD) measurements conducted on site. True distance from the hydrophone array to the playback source was measured using a Bushnell Elite 1500 7x26 Laser Rangefinder (accuracy ± 0.9 m over a range of 5-1465 m). Measurements were taken as often as possible, and the maximum interval between measurements was 3.5 min. Because distances were not measured continuously but the acoustic recordings were continuous, distances between measurements were linearly interpolated in MATLAB (version 7.0.4).

The depth of the playback source was measured continuously using a Suunto D3 digital dive watch. Distances up to 100 m and depths up to 27 m were tested. Sounds received with sufficient signal to noise ratio were localised and the difference between the localised position and the known position was calculated to estimate the accuracy of the acoustic localization method. The calibration demonstrated that the range calculated using the localisation method differed from true range on average by 12.6 ± 16.6 m (mean±stdv; n=54, 17 of which were tailslaps and the remaining 37 were burst-pulse calls and whistles). This corresponded on average to 23 ± 19 % of true distance. These errors may have resulted from the fact that natural sounds were used rather than man-made sounds that generally give smaller errors (e.g., Hastie et al., 2006). However, these are the most appropriate sounds to investigate the accuracy of the localisation method used. Errors of similar magnitude were found using other types of arrays when playing artificial sounds modelled on known delphinid signals (e.g., Quick et al., 2008).

Source level (SL) estimation

A calibrated received spectrum was calculated from the most intense 200 ms section of each sound, or the whole sound if its total duration was less than 200 ms. The received spectrum was calculated between 250 Hz and 48 kHz in 1/3 octave bands for the recordings using a sampling rate of 96 kHz. For recordings using a 192 kHz sampling rate the frequency bandwidth used to calculate the received spectrum was from 250 Hz to 70 kHz. Despite this difference in the frequency bandwidth, most of the energy in the signal was contributed from the octave bands containing the signal, therefore it should be possible to compare received levels calculated using different frequency bandwidths. Killer whale hearing is less sensitive below 1 kHz (Hall & Johnson, 1972; Szymanski et al., 1999), however some of the sound types analysed here, such as herding calls (see Chapter 4), had considerable energy below 1 kHz. The low-frequency cutoff of 250 Hz was chosen to provide a consistent frequency band to compare source levels across sound types.

Source level (SL) was calculated (in dB rms re 1 µPa at 1m) as:

$$SL = RL + 20\log_{10}(r) - k$$

where *RL* is the received level in dB, *r* is the range estimate in m and *k* is the near-field anomaly, assumed to be 3 dB following the method of Miller (2006). This value is likely overestimated for the frequency range of high frequency whistles. However, Marsh & Schulkin (1962) do not provide a value for such high frequencies (maximum is 10 kHz), so the 3 dB value was used for consistency. The broadband source level was calculated as the sum of the calibrated source spectrum at each 1/3-octave band. As no correction for signaller orientation is possible using this method, the term 'apparent source level' is used (Møhl et al., 2000).

Active space estimation

Active space can be estimated using information on the signal source level, the hearing characteristics of the receivers, the sound propagation characteristics of the environment and the background noise in the environment. Information on the hearing sensitivity of killer whales was extracted from Hall & Johnson (1972) and Szymanski et al. (1999) and a weighting function was applied to it by Wensveen & Van Roij (2007). Because there are no measurements of critical ratios of killer whales, I judged a signal to be detected if the received level in at least one 1/3 octave band exceeded the hearing threshold or the background noise level after subtracting 6

dB from it, whichever was higher, following the method used by Miller (2006). The background noise in the environment used was that for sea states 0 and 6, extracted from Knudsen et al. (1948). Finally, the transmission loss (TL) in the environment was calculated using Marsh & Schulkin's (1962) model for shallow-water transmission:

$$TL = 15\log_{10}(r) + \alpha r + \alpha_T\left(\frac{r}{H-1}\right) + 5\log_{10}(H) + 60 - k_L$$

where r is the range estimated from the localisation analysis, α is the absorption coefficient in seawater, α_T is the shallow-water attenuation coefficient, H is the skip distance and k_L is the near-field anomally. The absorption coefficient α was calculated as $0.036 f^{1.5}$ dB.km^{-1} where f is the frequency in kHz (see Janik, 2000b). The values for α_T and k_L assuming a sand bottom and sea states of 0 or 5, and the equation to estimate H are given in Marsh & Schulkin (1962). Since no values were given for sea state 6 in Marsh & Schulkin (1962) the values for sea state 5 were assumed for the high background noise conditions. For frequencies higher or lower than those given in Marsh & Schulkin (1962) the values for the minimum and maximum frequency were assumed.

Results

A total of 9.5 hr of high-quality recordings meeting the localization criteria were collected in the presence of killer whales over 5 days in 2008 and 9.3 hr of recordings were collected over 10 days in 2009. Of a total of 419 high frequency whistles detected, 164 were of quality 1, 215 were of quality 2 and 40 were of quality 3. Forty-two high frequency whistles were localized. A total of 92 herding calls were detected and of these 11 were localized. A total of 7203 burst-pulse calls were detected, of which 4622 were of quality 1, 2030 of quality 2 and 199 of quality 3; the remaining 352 were of varying quality. Only calls of quality 2 or 3 were used in the localisation analysis, and 114 of these were localised. Figure 3.4 shows example spectrograms of each sound type.

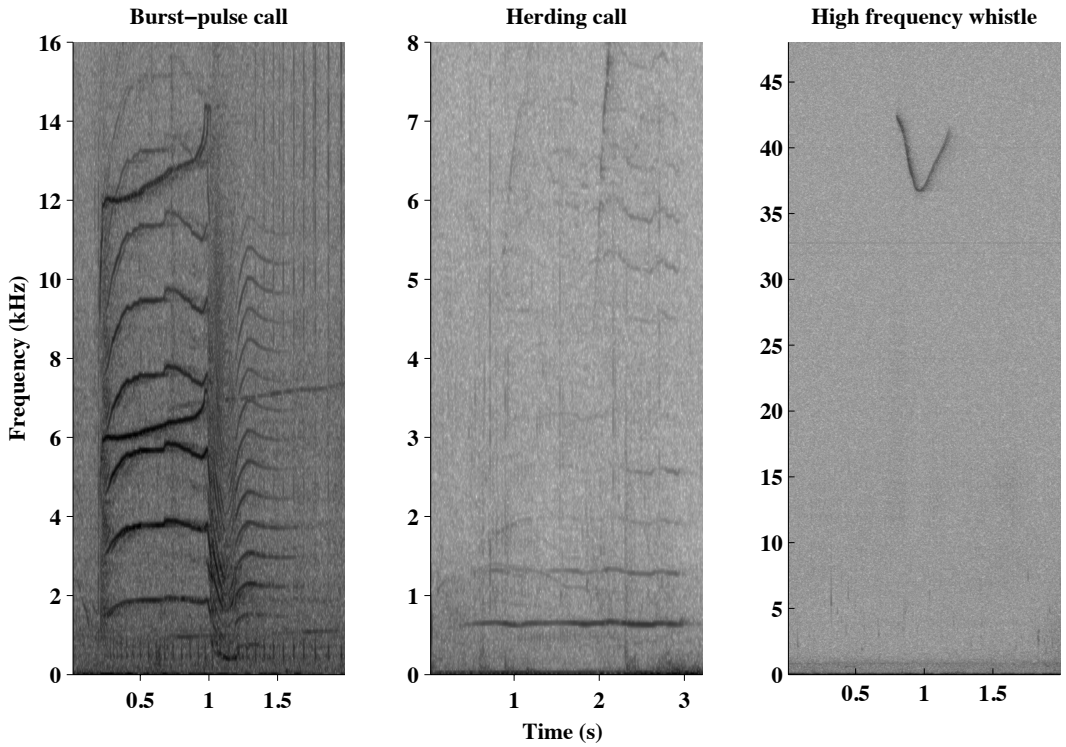

Figure 3.4. Example spectrograms of burst-pulse call (biphonic call), herding call and high frequency whistle. Note the y-axis scale changes between spectrograms.

Most sounds that were not localized were due to poor signal to noise ratios or the presence of overlapping sounds. This was especially true for burst-pulse calls, where the presence of many overlapping calls or echolocation clicks made it difficult to select an appropriate section for localisation. Only signals detected on all four hydrophones were considered for estimation of source position and only signals localised up to 200 m (approximately four times the maximum dimensions of the array) were used, because accuracy of localisation is known to deteriorate quickly with distance from the array (Watkins & Schevill, 1972).

The estimated locations in the water column for each sound type are shown in Figure 3.5. Most of the localised sounds were within 100 m of the array and had a widespread distribution across depths. On the other hand, sounds localised beyond 100 m tended to be nearer the sea surface.

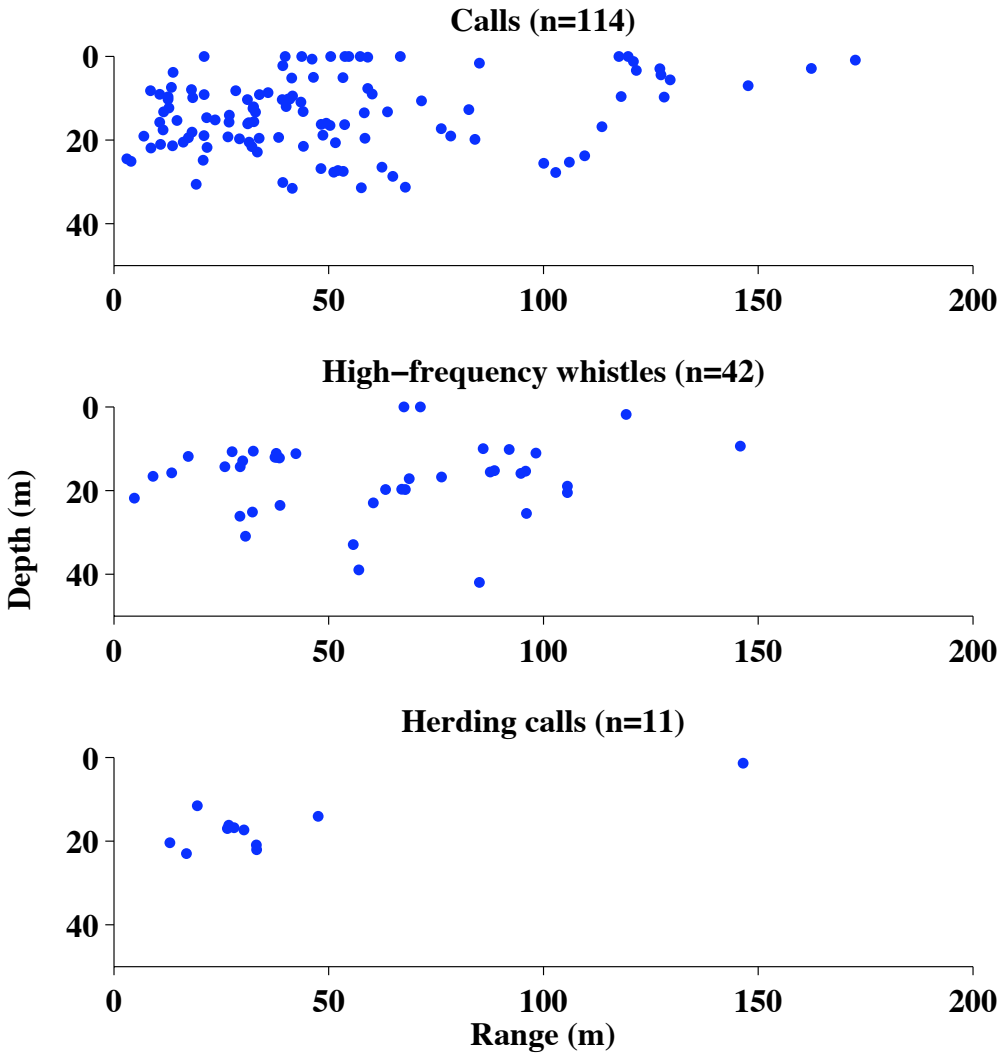

Figure 3.5. Estimated depths and ranges of localized sounds. The vertical hydrophone array was generally positioned at 10, 20, 30 and 40 m.

The estimated apparent source levels of burst-pulse calls and high frequency whistles had similar distributions (Figure 3.6). Burst-pulse calls had the highest mean apparent source level (144 ± 8 dB re 1 µPa @ 1m), followed by high frequency whistles (142 ± 9 dB re 1 µPa @ 1m), with herding calls being the least intense (140 ± 8 dB re 1 µPa @ 1m). The maximum apparent source level estimated of a burst-pulse call was 166.6 dB, of a high frequency whistle was 160.5 dB and of a herding call was 155.2 dB. While the distributions of apparent source levels of calls and high frequency whistles showed a peak around 140 dB, the distribution of source levels of herding calls did not have a peak, probably reflecting the smaller data set.

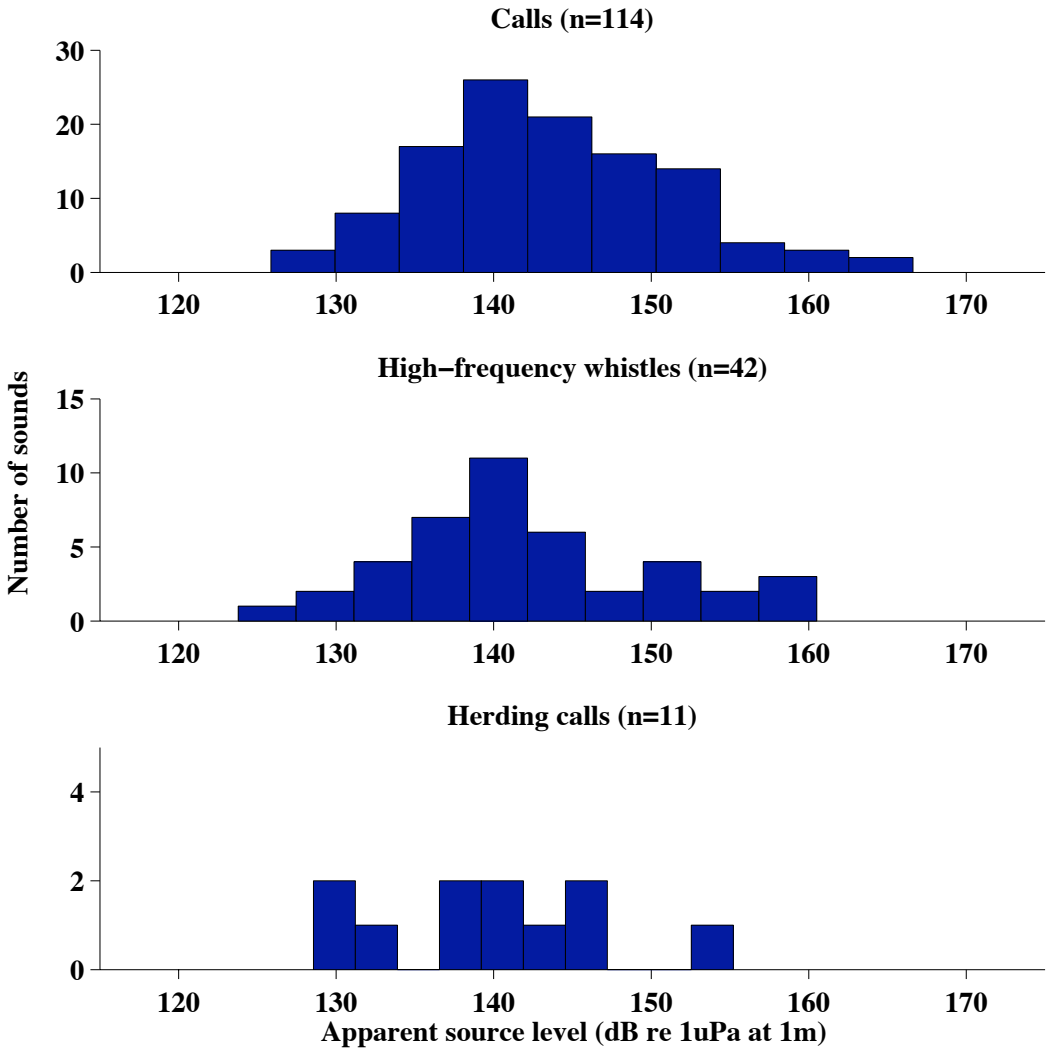

Figure 3.6. Apparent source levels of burst-pulse calls, high frequency whistles and herding calls.

High frequency whistles and burst-pulse calls had similar average source levels, however this resulted in slightly higher active spaces for high frequency whistles. The maximum active space of a call obtained was 23.8 km in sea state 0 noise conditions, while the maximum of high frequency whistles was 4.9 km (Figure 3.7). The call with the largest active space was also one of the calls with the highest source level and was a biphonic call.

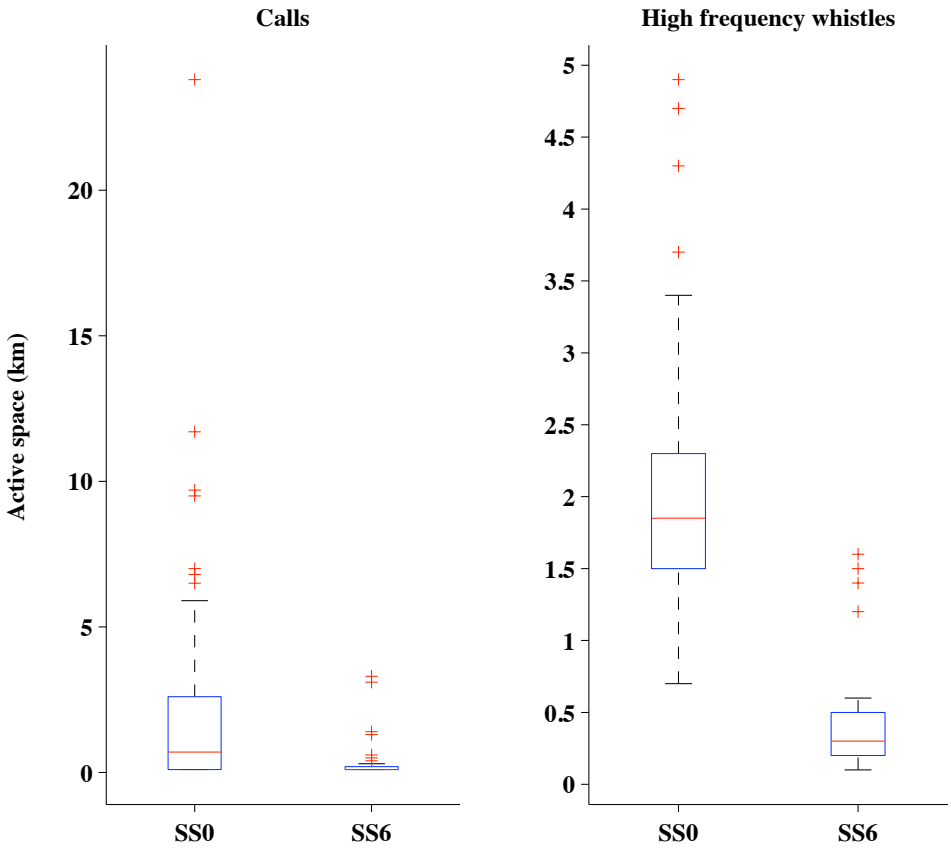

Figure 3.7. Distribution of active spaces of calls and high frequency whistles in sea state 0 noise conditions (SS0) and sea state 6 noise conditions (SS6). Note that the y-axis values are different.

On average, high frequency whistles had an estimated active space of 2.1 ± 1 km in sea state 0 noise conditions, while burst-pulse calls had an average active space of 1.9 ± 3.1 km in the same background noise conditions. However, both sound types had greatly reduced active spaces in sea state 6 noise conditions (Figure 3.7). High frequency whistles had an estimated active space of 0.48 ± 0.45 km, while the active space for burst-pulse calls decreased to 0.25 ± 0.45 km. Herding calls had the lowest active space with an average of less than 0.1 km even in sea state 0 noise conditions, because signal detection of these low-frequency signals was predicted to be limited by the threshold of audibility.

Discussion

Killer whales in this study produced burst-pulse calls, high frequency whistles and herding calls with varied apparent source levels however the range of levels estimated was similar across sound types (Figure 3.6). Herding calls had the lowest average source level, followed by high frequency whistles and burst-pulse calls. The

average apparent source levels of burst-pulse calls and high frequency whistles were similar and resulted in similar active spaces despite the substantial differences in frequency of the signals. Although killer whales are more sensitive to the frequency band of high frequency whistles than that of burst-pulse calls (Szymanski et al., 1999), the higher frequencies suffer greater effects of absorption and do not propagate as far, thus constraining the active space of higher frequency signals. The distribution of call source levels reported here is substantially less than the distribution of call source levels reported for killer whales in British Columbia, although the maximum values did not differ (Schevill & Watkins, 1966; Miller, 2006; Holt et al., 2009).

Errors in the source levels in this study could have originated from the assumptions used throughout the calculations. First, the hydrophone sensitivity was assumed to be that reported by the manufacturer. It is possible that, particularly at the higher frequencies (>30 kHz), this sensitivity is overestimated. If so, the source levels reported here, particularly for high frequency whistles that generally had most energy above 30 kHz, are an underestimate. Based upon some of the calibrations, this error may be up to ±20 dB. On the other hand, the source levels of lower frequency sounds, such as herding calls and other burst-pulse calls, is most likely accurate to within ±10 dB. Future calibrations of the equipment used to make the recordings will allow for an improvement in the source level estimates reported here.

The range estimate, which is determined by the sound speed and the time-of-arrival differences (TOADs), could have errors resulting from inaccurate estimates of temperature and water salinity. This would lead to errors in the sound speed estimation. Because the temperature and salinity were not measured at the time of recordings, use of average values used could have introduced a source of error. Second, the transmission loss model used could be inappropriate. It would have been desirable to conduct transmission loss measurements in the recording area to eliminate this potential source of error. Understanding the localisation accuracy of the method used would also have benefited if the calibration had been conducted at the site where the data were collected, because differences in environmental characteristics and topography will influence transmission paths (see review in Spiesberger & Fistrup, 1990). Finally, it is possible that the source levels reported here were underestimated due to the orientation of the signaller, which was unknown, particularly for the higher frequency signals. Delphinid whistles and killer whale

biphonic calls are directional signals (Miller, 2002; Lammers & Au, 2003) and the orientation of the signaller will influence the source level estimates.

There are also uncertainties in the estimates of active space. If the signals are produced with directionality the orientation of the signaller will affect the maximum distances over which they can be detected depending on the orientation of the signaller. On the other hand, the directional properties of the hearing mechanism will also influence the range over which signals can be detected and how those signals will be detected (Bain & Dalheim, 1994). If there is directionality in the hearing mechanism of killer whales, the detection of signals at maximum ranges will be a result of the interaction between the emitted beam and the receiving beam (Lammers & Au, 2003). The noise level in the environment was assumed to be similar to that measured in other locations (Knudsen et al., 1948) but this could have introduced another source of error. Changes in background noise, for example caused by shipping traffic and by other whales vocalising, will also affect a signal's maximum active space. It is possible that killer whales in this area change signal source level according to background noise characteristics, as shown elsewhere (Holt et al., 2009), nevertheless the background noise characteristics may affect signal perception. Finally, even if the signal can be detected at certain ranges, more information on the signal parameters that are relevant for killer whale communication and how these are transmitted (and degraded) through the environment is necessary to understand if the signals would be accurately perceived even at their maximum active space ranges.

Nevertheless, since many of the assumptions made here were the same as those of Miller (2006) it is possible to draw some comparisons between the estimated source levels of calls from both studies. The estimates of apparent source level reported by Miller (2006) were similar to other estimates of source level of killer whale calls in the Northeast Pacific (Schevill & Watkins, 1966; Holt et al., 2009). However, in this study the average call source level was 144 dB, lower than any of the previous estimates for killer whales elsewhere. In general, calls in this study had a distribution of source levels more similar to the least intense call types recorded from killer whales in British Columbia (Figure 4 in Miller, 2006).

The considerably lower estimates of active space of burst-pulse calls reported here relative to those reported for killer whales in British Columbia are most likely a result of the lower source levels estimated. Indeed, Miller (2006) estimated a decrease of 24-30% in active space estimates with a 6 dB decrease in source level of long and

short-range calls. The source levels of calls reported in this study were on average approximately 9 dB lower than those reported by Miller (2006). In addition, the water depth in this study area was shallower than that in British Columbia and, as reported by Miller (2006), a decrease in water depth will also lead to a decrease in estimated active spaces. Therefore, the short active spaces reported in this study suggest that in comparison to calls produced by killer whales in British Columbia, calls produced by killer whales in Iceland are relatively short-range calls.

The majority of calls (~90%) analysed here were single-component calls that were probably produced during foraging, because this was one of the most common activities observed during recordings. The conclusion that these are short-range calls is in agreement with Miller 's (2006) analysis of single-component calls in British Columbia, although the source levels reported here are approximately 5 dB lower than those reported in Figure 4 of Miller (2006). The source levels of high frequency whistles reported here are not comparable to high frequency whistles produced by killer whales elsewhere, because to date these sounds have only been recorded in the Northeast Atlantic (Chapter 2) and no estimates of source levels were conducted in other areas. Nonetheless, the whistle source levels reported here are similar to the average source levels of the lower frequency whistles reported from British Columbia (Miller, 2006). In comparison with other delphinid whistles, the source levels obtained here were lower than those obtained for spinner dolphin whistles, that had a mean source level of 150-154 dB (Lammers & Au, 2003), and lower than the range of 134-169 dB obtained for bottlenose dolphin whistles (Janik, 2000b). Rasmussen et al. (2006) reported whistle source levels for whitebeaked dolphins in the range of 118-167 dB, which overlaps the ranges of source levels obtained here.

It is likely that the source level of whistles changes with behavioural context (Rasmussen et al., 2006; Janik, 2009). For example, spinner dolphins were reported to produce whistles with source levels between 109-125 dB during the day while resting (Watkins & Schevill, 1974). Therefore, some of the variability in high frequency whistle source levels may be explained by recordings conducted in different behavioural contexts. However, it is possible that the overall small sample sizes of high frequency whistles in the present study means that this sample is not representative of the source levels produced. The fact that most of the localised whistles had fundamental frequencies above 30 kHz (see Chapter 4) suggests that high frequency whistles with frequencies between 17-30 kHz may have been

underrepresented. The uncertainties about the sensitivity of the hydrophones used will also undoubtedly affect the source level and consequently the active space estimates. Nevertheless, based on results obtained so far it seems that high frequency whistles are relatively short-range signals used in communication most likely within a group, similar to what was proposed for the lower frequency whistles produced by killer whales (Thomsen et al., 2002). Nevertheless, as only a relatively small sample of sounds was localised, it is possible that the estimated source levels and active spaces reported here are not representative of what is produced by killer whales in this area.

The apparent source levels of herding calls were lower than those previously reported in the same area (Simon et al., 2006). The previous estimates were based on observed distances from the signaller (Simon et al., 2006), instead of localisation analysis as conducted in this study. Nevertheless, it is possible this difference could have resulted from errors in range estimation in the localisation analysis conducted here. Sounds with constant frequency generally result in higher localisation errors than frequency-modulated sounds (McGregor et al., 1997). The herding call is characterised by a low and constant frequency (Simon et al., 2006) and it was more difficult to localise than other sounds, which resulted in a smaller sample size. It is possible that the herding calls have indeed much higher source levels than those reported here. Nevertheless, their active space will constrained by the very low hearing sensitivity of killer whales at frequencies below 1 kHz (Szymanski et al., 1999) and most likely this call functions in prey manipulation, as previously suggested (Simon et al., 2006).

This study suggests that burst-pulse calls and high frequency whistles produced by killer whales in Iceland are used as short-range signals for communication within a group, although as mentioned above there are potential caveats to these estimates that future studies should address. Though high-source level signals were rarely produced (maximum call source level was ~167 dB), the typical source level of calls was much lower than the maximum detected levels. Most of these sounds were recorded in feeding contexts in which group members are typically at close ranges and therefore there may not be a need for long-range signalling. The intense long-range signals reported by Miller (2006) are thought to be typically produced during behavioural contexts in which group members are dispersed and out of visual range (Ford, 1989). In contrast, visual observations in Iceland suggest that group members are rarely more than a few body lengths from each other. Therefore, killer whales feeding upon

spawning herring may not benefit from the production of intense signals to remain in contact or maintain group coordination, because the typical distance between group members are in the order of tens of meters.

In herring overwintering grounds different groups may communicate with each other to join into a larger group size. This may make it easier to cooperatively force herring from deeper waters (Nøttestad et al., 2002) or to feed upon a large herring school. However, though it is possible that other groups are attracted by the sounds produced by a feeding group (Shapiro, 2008), cooperative feeding between different groups is not commonly observed (Similä & Ugarte, 1993; Bisther & Vongraven, 1995; Bisther, 2002). In fact, occasionally killer whale groups appear to compete for prey resources and feeding groups can be displaced from a prey patch by approaching groups (Bisther & Vongraven, 1995; Bisther, 2002). In these cases, if the incoming group eavesdropped on acoustic stimuli produced by the feeding group and was attracted to it, sound production by the feeding group may have incurred the cost of increased competition for prey and possibly losing access to prey entirely.

In species that use sound during foraging, it can be difficult to determine whether the function of a signal is primarily for prey detection and manipulation, in which attraction of conspecifics is a by-product, or whether its real function is in attracting other conspecifics (e.g., Janik, 2000a). In low background noise conditions it is likely that calls and high frequency whistles will propagate further and may be detected by conspecifics. In Iceland, active foraging periods can be quite short in duration and group sizes are small compared to observations from carousel feeding episodes in Norway. Overwintering herring in Norway may consist of large aggregations, with corresponding benefits to larger predator group sizes. If so, we might expect call characteristics, and specifically source levels and active space, to differ between killer whales in Iceland feeding upon spawning herring and those in Norway feeding upon overwintering herring. In the future, direct observations of the consequences of conspecific approaches for feeding groups may shed some light into the benefits the signaller may gain by producing signals intense enough to be detected by other groups. Ultimately testing prey and conspecific reactions to feeding-related signals will be essential to elucidate their function.

Chapter 4

Depth of sound production by fish-eating killer whales (*Orcinus orca*) off Iceland

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Introduction

Marine mammals exhibit complex foraging behaviours to exploit the three-dimensional distribution of their prey and their use of the water column is likely determined by the prey distribution and foraging strategies employed (Davis et al., 2007). These predators are limited by their need to come to the surface to breathe and can only be submerged for a limited amount of time that is related to their body size and physiology (Noren et al., 2002). Therefore, their use of the water column will also be limited by their diving capabilities and physiology.

In some cases, sound production is related to the foraging strategies employed by these animals. In such cases, knowing the depth of sound production gives information on how animals use the water column. For example, bottlenose dolphins *Tursiops truncatus* produce bray calls, low-frequency signals thought to be important in manipulating prey (Janik, 2000a). When sound production in the water column was investigated it was shown that, despite regularly diving near the seabed, production of bray calls, and consequently presumed feeding events, appeared to occur primarily at a narrow depth range in the middle of the water column (Hastie et al., 2006).

The underwater environment imposes constraints on the transmission properties of signals, and the depth of an underwater source is an important determinant of how the sounds will propagate (Urick, 1982). For example, sounds produced close to the surface will suffer degradation from surface reflections. It has been suggested that baleen whales use the deep sound channel, a channel in deeper waters where sound attenuation is minimal, in long-distance communication (Payne & Webb, 1971). In areas of ice cover, harp (*Pagophilus groenlandicus*) and Weddell (*Leptonychotes weddellii*) seals produce most sounds below the underface of the ice, most likely to avoid attenuation from the ice cover in transmission of signals (Moors & Terhune, 2005). Therefore, animals may actively choose a depth from which emitted signals are more likely to be transmitted over intended distances. Alternatively, if the depth of

sound production is proscribed by ecological factors, like the depth of prey, then the depth of the prey may have secondary consequences for the way in which the signal propagates away from the calling predator.

The sound production mechanism of signallers likely constrains the signals that can be produced, though cetacean sound production mechanisms are still not completely understood. There is strong evidence that odontocete clicks are produced in the nasal passages and then radiate through the melon (Cranford et al, 1996; Cranford, 2000). Whistles also seem to be produced in the nasal passages (Dormer, 1979; Ridgway et al., 1980) but it is not known if they are produced by the same mechanism used to produce other signals, such as burst-pulse calls. Reports of individuals producing different sounds simultaneously (e.g., Miller & Bain, 2000; Corkeron & Van Parijs, 2001) suggest the existence of at least two independent sources (Dormer, 1979). The frequency content of emitted signals will be determined mainly by the oscillating source of sound production, but it may also be influenced by the resonating structures involved in sound propagation (source-filter theory; Kent & Read, 1992). In cetaceans, structures such as the nasal air sacs, may act as resonators (Ridgway et al., 1980) and if their size changes these may influence the frequency content of emitted signals.

With increasing pressure at deeper depths air-filled cavities will be compressed. If such cavities play a role in sound production, then the depth of sound production could have important effects on the sounds produced by cetaceans. For example, the peak frequency of whistles produced by belugas (*Delphinapterus leucas*) increased with increasing depth of whistle production while whistle amplitude decreased (Ridgway et al., 2001). However, whistle duration did not change with depth, although depth should have a more pronounced effect on the duration of longer signals (Ridgway et al., 2001). On the other hand, the duration and energy content of pilot whale (*Globicephala macrorhynchus*) calls decreased with increasing depth (Jensen et al., 2011a).

Increasing pressure with increasing depth also limits the amount of air volume available for sound production, assuming an air-driven source. For example, the number of clicks produced by sperm whales in a block of clicks decreases with increasing depth, which likely reflects the decreasing air volume available for sound production (Wahlberg, 2002). Finally, auditory sensitivity may also be affected by increasing depth. Changes in hearing sensitivity have been observed in California sea

lions (*Zalophus californianus*; Kastak & Schusterman, 2002) but not in belugas (Ridgway et al., 2001) most likely reflecting the differences in the hearing mechanisms of the two species.

Understanding the depth at which sounds are produced can give us information on how animals use the water column, how depth may affect signals produced and what functions signals may have. For example, despite diving to considerable depths, Weddell seals only vocalised during ascent and at shallow depths near breathing holes (Evans et al., 2004). The repetition rate of sounds produced increased with decreasing distance to the breathing hole suggesting that the sounds may have been used for some sort of navigation (Evans et al., 2004).

Killer whales in Iceland feed on Icelandic summer-spawning (ISS) herring (*Clupea harengus*) and produce two feeding-related sounds: tailslaps and herding calls. Tailslaps are produced to stun the herring which killer whales then consume one by one (Similä & Ugarte, 1993; Simon et al., 2005). Herding calls are long, low frequency sounds thought to be used to help herd the herring just before a tailslap (Simon et al., 2006). Killer whales also produce burst-pulse calls and high frequency whistles (Chapter 2) but the function of these sounds is still little understood. If production of calls and high frequency whistles is important in a feeding context these may be produced at the same depths as feeding-related sounds.

The frequency content of killer whale calls seems to differ between adult males and adult females, suggesting that resonant structures may vary in size and correlate with overall body size (Miller et al., 2007). However, the effects of depth on sound production by killer whales are little understood.

Here, I investigate the depth of sound production by killer whales in a spawning ground of ISS herring to investigate the possible functions of the different sound types. I then examine sounds produced at known depths to investigate if signal parameters are influenced by the depth of sound production.

Methods

This study was conducted in Vestmannaeyjar, Iceland, in July 2008 and 2009. Acoustic recordings were collected using a 4-element vertical hydrophone array and detected sounds were acoustically localised (see Chapter 3 for details of recording system and analysis). In addition to the localised sounds used in Chapter 3, tailslaps were also localised and reported here. To investigate the depth of sound production,

the depth distribution of tailslaps, herding calls, burst-pulse calls (henceforth referred to simply as "calls") and high frequency whistles was calculated.

The calibration experiment conducted to estimate the accuracy of the localisation method demonstrated that the estimated depth differed from true depth by 5.1 ± 5.0 m (mean±stdv; *n*=54 localised sounds, 17 of which were tailslaps and the remaining 37 were burst-pulse calls and whistles; Chapter 3) on average. Therefore, in cases where the estimated depth of the signaller was up to 5m above the surface, the signaller was assumed to be at the surface.

To investigate whether the depth of sound production influenced the sounds being produced, descriptive parameters were extracted from each sound type. Only calls, herding calls and high frequency whistles were considered in this analysis. The fundamental frequency contour of high frequency whistles was extracted using a peaks contour extraction algorithm (see the Methods of Chapter 2 for details). From each contour the minimum and maximum frequency as well as duration were extracted. Peak frequency was extracted by generating a power spectrum for each whistle and measuring the frequency of maximum power, using Matlab 7.11 (R2010b).

Spectrograms were generated in Matlab 7.11 (R2010b, spectrogram parameters: FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; overlap=87.5%; window function=Hann; frequency resolution=46.9 Hz; time resolution=2.67 ms) in order to measure the parameters from herding calls and other burst-pulse calls; parameters were extracted directly from the spectrogram using the cursor. For herding calls the minimum, maximum and peak frequencies as well as the duration were extracted. Peak frequency was extracted as explained above for high frequency whistles. All parameters were extracted from the fundamental frequency contour. This was always the one containing most energy in herding calls, even when harmonics were present.

The duration and minimum and maximum frequency of the fundamental frequency of calls were also measured. However, the amount of energy across harmonics can vary within and between calls (Miller et al., 2007). To account for that, each call was divided into 0.05 s time intervals and the peak frequency was calculated for each time interval, as explained above. The maximum peak frequency for each call was then calculated.

To evaluate the relationship between characteristics of sounds produced and the depth of sound production, scatter plots were generated in Matlab 7.11 (R2010b) and linear models were fitted to these using R 2.11.1 for Mac OS (R Development Core Team, 2010). Bonferroni corrections were applied because multiple tests were conducted for each sound type, therefore the significance level of 0.05 was divided by the number of tests conducted for each sound type.

Results

A total of 9.5 hrs (on 5 different days) and 9.3 hrs (on 10 days) of recordings were collected in 2008 and 2009 respectively. Of a total of 419 high frequency whistles detected, 164 were of quality 1, 215 were of quality 2 and 40 were of quality 3 (see Chapter 2 for definition of quality scores). Forty-two of the total 419 high frequency whistles were localized. A total of 92 herding calls were detected and of these 11 were localized. A total of 7203 burst-pulse calls were detected, of which 4622 were of quality 1, 2030 of quality 2 and 199 of quality 3, while the remaining 352 were of varying quality. Only calls of quality 2 or 3 were used in the localisation analysis, and only 114 of these were localised. Finally, of a total of 190 tailslaps detected only 12 were localised. Most sounds were not localized due to poor signal to noise ratios or overlapping sounds. This was especially the case for burst-pulse calls, where the presence of many other calls or echolocation clicks made it difficult to select an appropriate section for localisation. Additionally, only signals localised up to 200 m (approximately four times the maximum dimensions of the array) were analysed, because the accuracy of localisation is known to deteriorate quickly with distance from the array (Watkins & Schevill, 1972).

Depth of sound production

The depth of sound production for calls, high frequency whistles, herding calls and tailslaps was estimated from the localisation analysis. Figure 4.1 shows the distribution of depth of production of these different sound types.

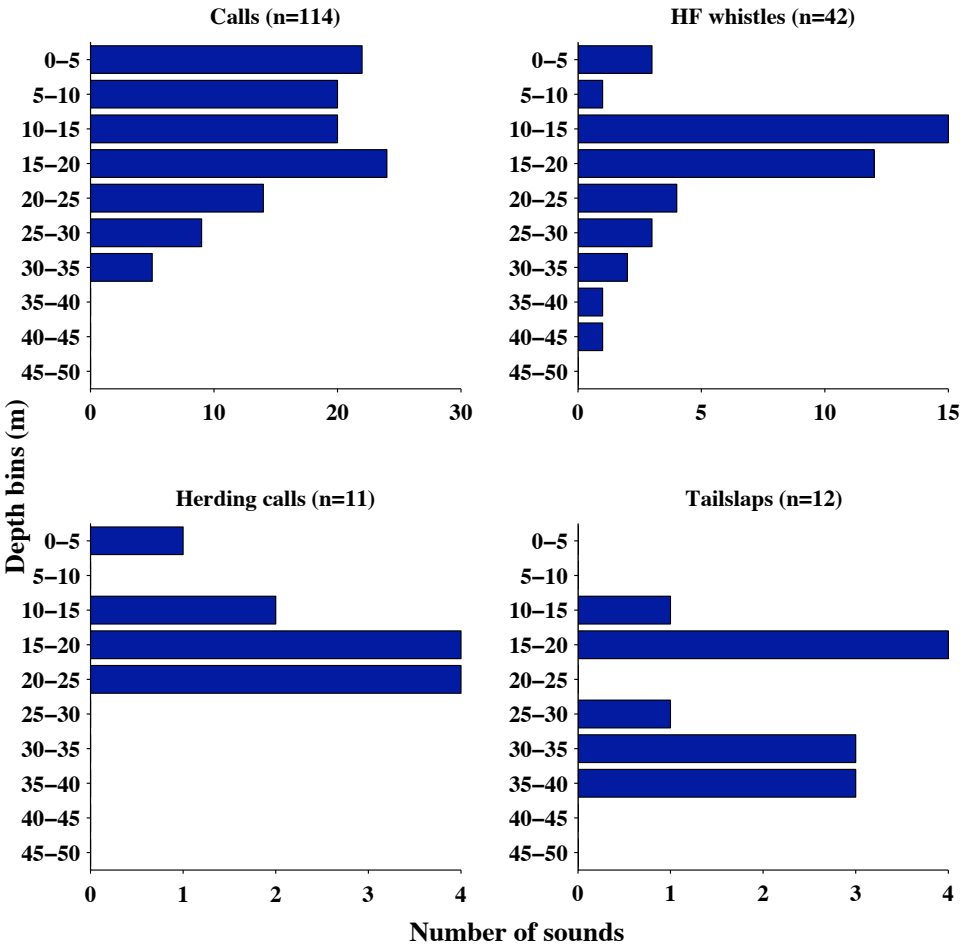

Figure 4.1. Frequency distribution of the depth of localized calls, high frequency whistles, herding calls and tailslaps. Sample sizes are included inside brackets.

In general, calls were mostly produced between the surface and 20 m depth, and the maximum depth was 31.6 m. High frequency whistles showed a peak of production between 10 and 20 m; the number of high frequency whistles localised decreased with depth below 20 m. However, the deepest whistle localised was at a depth of 42 m. In contrast, localizations of both herding calls and tailslaps had more restricted distributions. Herding calls were mostly produced between 10 and 25 m depth. Tailslaps had two apparent peaks of production, one between 10 and 20 m and another between 25 and 40 m, however this may have been a result of the low sample size.

The depth distribution of calls and all other sounds was compared using Kolmogorov-Smirnov tests. Calls had a significantly different depth distribution to high frequency whistles (Kolmogorov-Smirnov test statistic=0.27; p=0.02) and tailslaps (Kolmogorov-Smirnov test statistic=0.53; p=0.003). Herding calls also had a

significantly different distribution to tailslaps (Kolmogorov-Smirnov test statistic=0.58; p=0.02).

Effects of depth on sound production

Sound parameters (mean ± standard deviation) from each sound type were extracted and are presented below. For herding calls, mean duration was 2.94 ± 1.18 s (range: 1.36-5.7 s; *n*=11), mean minimum frequency was 584 ± 32.3 Hz (range: 519-621 Hz), maximum frequency was 817 ± 50.3 Hz (range: 753-914 Hz), and peak frequency was 693 ± 25.9 Hz (range: 648-734 Hz). The duration and peak frequency of herding calls measured in this study was very similar to those reported by Simon et al. (2006).

Figure 4.2 shows the variation in each of the measured sound parameters with depth. There is a tendency for herding calls to increase in duration with increasing depth, although this relationship is very influenced by one short-duration call localised shallower than 10 m depth. The regression explained 22% of the variation in the data. Between 10 and 25 m depth, where most calls were produced, the duration varied considerably. Minimum and maximum frequencies show some variation that does not seem to correlate with depth. Indeed, both regressions were a poor fit to the data explaining less than 1% of the variation ($R^2 < 0.01$). Finally, peak frequency appeared to decrease slightly with depth, although the range of variation fell within 100 Hz. This regression also explained 22% of the variation in the data.

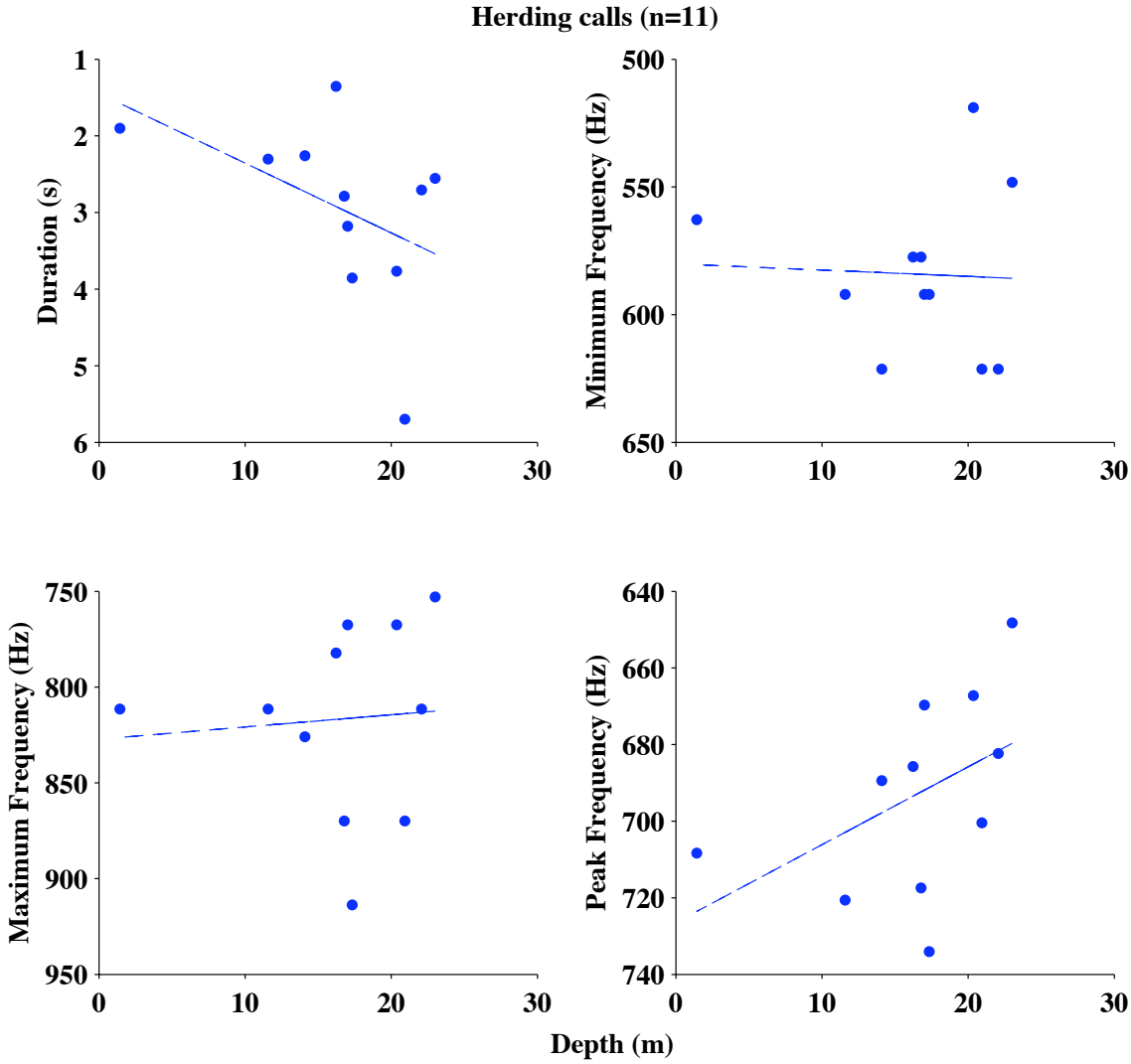

Figure 4.2. Variation in sound parameters of herding calls with depth. Sample size of herding calls analysed is given inside parentheses. Plots display variation in duration ($R^2 = 0.22$), minimum frequency ($R^2 = 0.002$), maximum frequency ($R^2 = 0.006$) and peak frequency ($R^2 = 0.22$) of herding calls.

For high frequency whistles mean duration was 0.097 ± 0.113 s (range: 0.008-0.479 s), mean maximum frequency was 41.07 ± 6.57 kHz (range: 27.84-61.92 kHz), mean minimum frequency was 34.22 ± 6.67 kHz (range: 23.20-55.64 kHz) and mean peak frequency was 37.44 ± 6.29 kHz (range: 25.50-57.00 kHz). The duration was slightly lower than the overall mean for the entire sample of high frequency whistles recorded from Iceland (see Table 2.2 in Chapter 2), while the minimum and maximum frequencies were slightly higher. This suggests that localised whistles may not be fully representative of the entire repertoire of high frequency whistles produced by killer whales in this area.

Figure 4.3 shows the variation in measured high frequency whistle parameters with depth. Only duration seemed to increase with increasing depth. All frequency parameters seemed to decrease slightly with increasing depth. However, none of the regressions was a good fit to the data ($R^2 < 0.1$). Linear models of the log-transformations of all parameters were conducted, using a significance value of 0.0125, after Bonferroni correction. Log-transformations ensured that duration and minimum frequency followed a Normal distribution (Wilk-Shapiro test $p>0.1$). Although peak and maximum frequency were closer to a Normal distribution by visual inspection, these parameters were still significantly different from a Normal distribution (Wilk-Shapiro test $p<0.1$). The linear models showed that depth was only a nearly significant predictor of log-duration ($t_{40}=-2.5$; $p=0.02$).

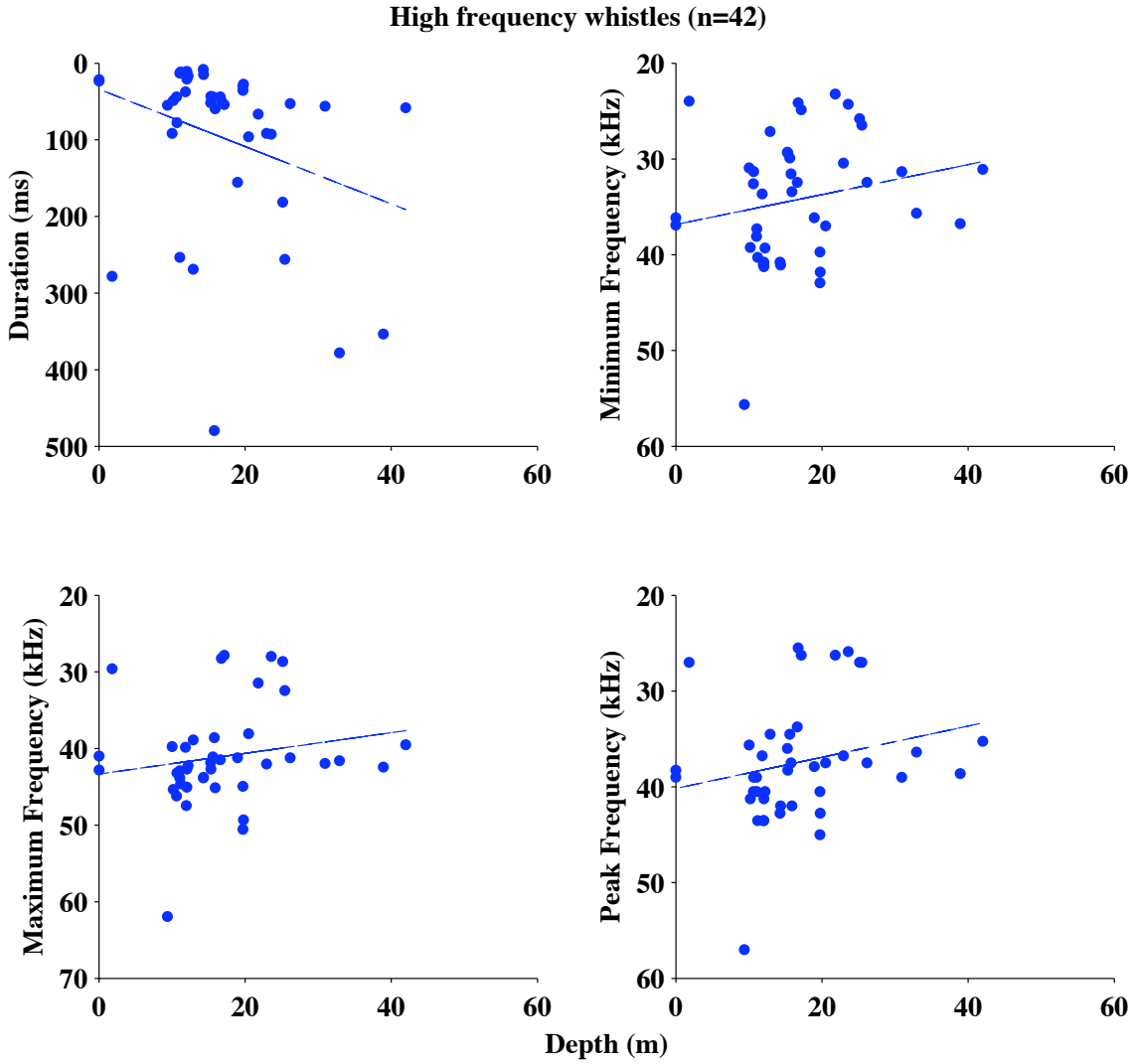

Figure 4.3. Variation in sound parameters of high frequency whistles with depth. Sample size of high frequency whistles analysed is given inside parentheses. Plots display variation in duration ($R^2 = 0.08$), minimum frequency ($R^2 = 0.04$), maximum frequency ($R^2 = 0.03$) and peak frequency ($R^2 = 0.05$) of high frequency whistles.

Finally, burst-pulse calls had a mean duration of 0.9 ± 0.5 s (range: 0.3-4.1 s), mean maximum frequency of 2.3 ± 2.0 kHz (range: 0.3-14.6 kHz), mean minimum frequency of 0.9 ± 1.2 kHz (range: 0.1-6.8 kHz) and mean maximum peak frequency of 3.82 ± 2.29 (range: 0.86-13.55).

Figure 4.4 shows the variation in measured parameters of burst-pulse calls with depth. There were no clear patterns in the relationship between depth and measured call parameters. Although all parameters seemed to slightly increase with increasing depth, the regressions were a poor fit to the data, generally explaining less than 10% of the variation in the data ($R^2 < 0.1$). Linear models of the log-transformations of all

parameters were conducted, using a significance value of 0.0125, after Bonferroni correction. These models showed that depth was a nearly significant predictor of maximum frequency (t_{111}=2.5; p=0.02), however it only explained 5% of the variation in the data. The normality assumption was not always satisfied by the log-transformation of frequency and duration parameters (Wilk-Shapiro test p<0.05), nevertheless it always made the distribution of parameters more similar to a Normal distribution.

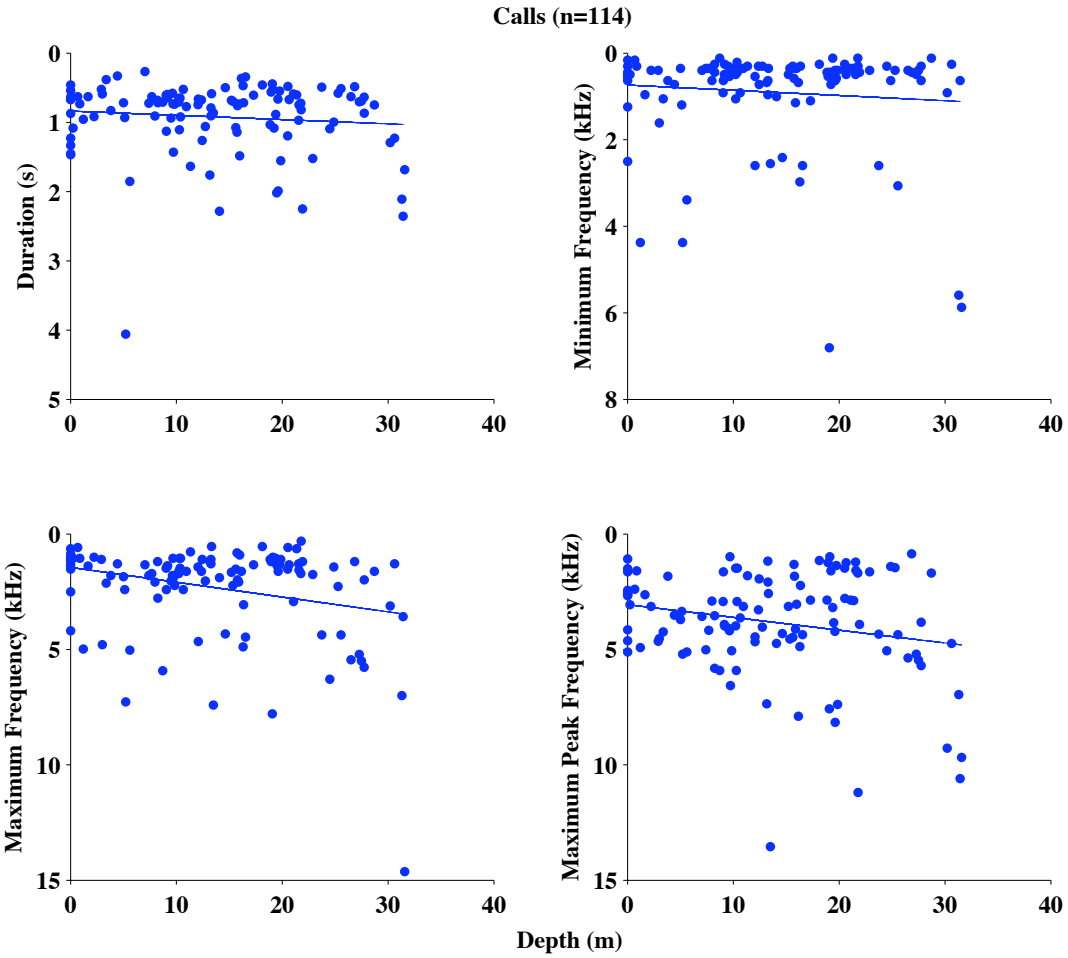

Figure 4.4. Variation in sound parameters of calls with depth. Sample size of calls analysed is given inside parentheses. Plots display variation in duration (R^2 = 0.01), minimum frequency (R^2 = 0.008), maximum frequency (R^2 = 0.08) and maximum peak frequency (R^2 = 0.04) of calls.

Discussion

This study shows that the depth at which killer whales produce sounds changes with sound type. While feeding-related tailslaps and herding calls were predominantly

produced between 10 and 40 m, calls and high frequency whistles had more widespread distributions. Calls and high frequency whistles were produced down to similar depths of feeding-related sounds but were mostly produced in the top 20 m of the water column. This suggests that while call and high frequency whistle production occurs at the same depths where feeding-related sounds are produced and, presumably, feeding takes place, they are also produced in shallower waters.

Although the behavioural context of sound production is not known for the calls and high frequency whistles localised here, it is likely that these sounds reflect a wider variety of behaviours than just feeding and that the observed variability is related to the depth of sound production. Indeed, killer whales in this area are known to increase production of sounds during feeding and other activities, including resting and socialising (Simon et al., 2007), which presumably occur at shallower depths. Therefore, some of the calls and high frequency whistles recorded here may have been produced in these behavioural contexts. Nevertheless, these results show that killer whales do not actively choose a particular depth to improve sound transmission, when producing calls and high frequency whistles, as other cetaceans may do (e.g., Frazer & Mercado, 2000).

The depth distribution of sounds is linked to the amount of time that signallers spend at different depths. Killer whales in this area are known to spend most of their time in depths of less than 10 m (Schorr et al., 2001), which is similar to other killer whale populations (Baird et al., 2005; Miller et al., 2010). If killer whales recorded during this study made a similar use of the water column, then the number of calls and high frequency whistles produced deeper than 10 m suggests that calling at depth is somehow relevant to these whales. It would be necessary to complement these results with direct measurements of the time spent at depth to understand if calling and high frequency whistle production occurs more frequently at particular depths. A method that allowed simultaneous monitoring of the time spent at depth by a signaller and the sounds produced at depth would be useful to understand killer whale calling behaviour (see Chapter 5).

There was a difference in production of calls and high frequency whistles at depths above 20 m. While calls were equally distributed between the surface and 20 m, high frequency whistles showed a peak between 10 and 20 m. This could be a result of the method used to localise these sounds. The vertical hydrophone array used consisted of four hydrophones, the first of which was generally at depths between 5

and 10 m. One of the requirements of the localisation analysis was that the signal needed to be clearly detectable on all four hydrophones. It is possible that high frequency whistles produced near the surface were more likely than other sound types to have insufficient amplitude at the more distant hydrophone, due to their high frequency content. Some errors also occurred in localising calls that were presumed to be near the surface, as the localisation resulted in positions up to 5 m above the water surface. These were assumed to be at the surface and reflect the difficulty in localising sounds produced at very shallow depths.

Depth of feeding-related sounds

The fact that most feeding-related sounds were produced at depths of more than 10 m, and some were produced down to approximately 40 m, suggests that feeding occurs below 10 m depth. This is in contrast to the know carrousel feeding technique used by killer whales in herring overwintering grounds, both in Norway and Iceland, where killer whales bring the fish all the way to the surface where feeding occurs (Sigurjónsson et al., 1988; Similä et al., 1996). Particularly in overwintering grounds in Norway, killer whales appeared to prefer feeding on herring schools found in shallower waters although schools of herring were also found at greater depths (Similä, 1997).

Fish jumping at the surface were never observed in the area where this study was conducted, also suggesting that feeding takes place at depth. As opposed to previous studies on the foraging behaviour of herring-eating killer whales (Similä et al., 1996; Domenici et al., 2000), this study was conducted on a herring spawning ground. Herring prefer shallow areas (usually less than 50 m deep) during spawning, and attach their eggs to gravelly material or seaweed forming a layer over the sea bottom (de Groot, 1980). It is possible that due to its life stage and the need to remain close to the seabed for spawning, herring are rarely found near the surface, and whales dive closer to the seabed to gather the fish they then feed upon. These results suggest that killer whales may employ a different foraging technique on herring spawning grounds than on overwintering grounds (Sigurjónsson et al., 1988; Similä & Ugarte, 1993). However, a more detailed study of the interaction between prey and predator would be necessary to confirm this.

Although tailslaps were produced at depths up to 42 m depth, no herding calls were localised at these depths. It is possible this is due to a limitation in the ability to

localise these calls accurately (Chapter 3). Hastie et al. (2006) reported larger errors when localising low-frequency bray calls produced by bottlenose dolphins than when localising clicks or man-made sources. However, the fact that localised herding calls match the depths of tailslaps, which are also known to be related to feeding, suggests that the lack of herding calls in deeper waters may be real. It is possible that herding calls are used only in shallower depths because they are used in conjunction with specific feeding behaviours that take place at these depths, and that different behaviours are employed in deeper waters where only tailslaps are produced. Herding calls are not recorded every time tailslaps are recorded (Simon et al., 2006), suggesting that there are some differences in their use across feeding events. Whether these differences relate to prey behaviour, feeding strategy, or because herding calls are only produced by certain killer whale groups is still unclear. More localisations of herding calls would be necessary to investigate if there is a consistent difference in the depth of production of tailslaps and herding calls. Alternatively, the sound production mechanism used to produce such long signals as herding calls may be constrained by depth.

Effects of depth on sound production

Depth appeared to have little effect on either the frequency or the duration characteristics of calls, herding calls and high frequency whistles. Variation in these characteristics was poorly explained by depth alone, as illustrated by the regressions applied to the data.

The fact that depth had little effect on the fundamental frequency characteristics of sounds analysed here is in agreement with what has been found in seals (Moors & Terhune, 2005) and other toothed whales (Ridgway et al., 2001; Jensen et al., 2011a). The fundamental frequency contour encodes information thought to be relevant for communication between individuals in other delphinid species. For example, bottlenose dolphins encode individual identity information in the fundamental frequency contour of signature whistles and this information is still present even when other features of the signal are removed or altered (Janik et al., 2006). Indeed, previous authors have suggested that since the fundamental frequency contour is under the signaller's control it will not be affected by increasing pressure in diving animals (Tyack, 2000; Tyack & Miller, 2002).

Killer whale calls have stereotyped time-frequency contours that may be used to transmit information on group membership (Ford, 1991; Deecke et al., 2000; Miller & Bain, 2000). They therefore may be under control of the signaller to ensure reliable information is transmitted. High frequency whistles have much simpler contours that are not group specific (Chapter 2), however the frequency characteristics of these sounds also did not vary consistently with depth. It is possible that the signaller also controls the frequency characteristics of high frequency whistles to ensure information encoded in the frequency contour is reliably transmitted. However, a better understanding of what information is transmitted in different signal parameters is necessary to investigate if maintaining whistle frequency characteristics is of relevance to the communication system of killer whales.

Herding call frequency characteristics are possibly also under control of the signaller, because maintaining a stable frequency contour may be important if they are used to manipulate herring (Simon et al., 2006). Herring have a well-developed sense of hearing and are most sensitive to frequencies up to approximately 1.2 kHz (Enger, 1967). Therefore, herding calls are presumably produced at a frequency that maximises their effects on prey, and it may be desirable to maintain a stable frequency, regardless of depth, to ensure they have the desired effect on prey. It is possible, nevertheless, that herring hearing changes with depth, in which case killer whales might have to adapt their herding calls to the frequency that maximises an effect on herring. However, the depth of production of herding calls did not vary as much as that of calls and high frequency whistles, so few effects of pressure would have been expected across the sample in this study.

The duration of sounds also seemed to change little with the localization depth across all signal types, which is similar to what was found in belugas (Ridgway et al., 2001) but not in pilot whales (Jensen et al., 2011a). However, it has to be taken into account that the depths considered here are much shallower than those to which pilot whales regularly dived (Jensen et al., 2011a). It is possible that depth effects upon duration of signals and even frequency characteristics are stronger beyond the depth thresholds that were not attained by the animals in this study. Therefore, it is possible that at the depths considered here the effects of increasing pressure upon signal duration are negligible.

The same conclusion also holds for peak frequency, which also did not show a clear relation with increasing depth for any of the sound types analysed. Pilot whales

calling at considerably greater depths did not show consistent differences in peak frequency (Jensen et al., 2011a). If resonant structures are involved in the production of sounds (Ridgway et al., 1980; Mackay & Liaw, 1981), either these are little affected by increasing pressures, as could be the case if resonance occurs in tissues (Cranford et al., 1996), or the whales have some way of compensating for those effects (Amundin, 1991). Although killer whales appear to have resonant structures that provide cues to the sex of a signaller (Miller et al., 2007), these do not appear to be affected by depth at the range of depths tested here. It is possible that the depths tested here were just too shallow to identify any effects. Additional parameters such as the relative intensity across harmonics used by Miller et al. (2007) could be analysed to investigate the effects of depth on sound production.

Chapter 5

Behavioural context of sound production by fish-eating killer whales (*Orcinus orca*) off Iceland

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Introduction

A description of the repertoire of sounds that a species produces in defined contexts allows researchers to formulate hypotheses about the potential functions of signals. The selection pressures acting upon signallers and receivers will depend on the context in which signals are produced (see review by Seyfarth & Cheney, 2003). Therefore studying the context of signal production helps predict what information in the signal may be beneficial for signallers to transmit, and what benefits signallers may gain by producing such signals.

Observational studies can provide baseline information about the contextual use of communication signals. By simultaneously recording the signals produced and the context in which they are produced, it is possible to develop hypotheses about the function of these signals. Ultimately these hypotheses should be tested by conducting playback experiments (e.g., Cheney & Seyfarth, 1982). However, a realistic response to a playback stimulus may only be elicited in an appropriate context. The baseline data collected during observational studies gives insight into the context in which communication occurs and is thus extremely important for the appropriate design of playback experiments. It is from extensive observational studies that hypotheses on the function of communication can be proposed and tested (Slater, 1999).

Studies of terrestrial species have led to the identification of several functional categories of signals including mate-attraction, courtship, territorial defence, threat, alarm, parent-offspring recognition, social recognition and food assembly (Bradbury & Vehrencamp, 1998). Most cetaceans, however, live in a marine environment in which they are exposed to very different selection pressures from terrestrial animals. The underwater environment favours acoustic communication and these animals have developed complex acoustic signalling systems (Tyack, 2000). However, in contrast to terrestrial species, the function of most cetacean vocalizations is still unknown and few playback experiments have been conducted (see Deecke, 2007). Undoubtedly this

dearth of information arises from the difficulty in observing cetaceans directly, because they spend the majority of their time underwater (but see Herzing, 1996).

Long-term studies have only been possible for a few species that occur predictably in known areas and for which sufficient knowledge has been gathered for hypotheses on function to be proposed (Tyack, 1986b). Such studies have made it possible to use surface behaviours to define general behavioural categories (Mann, 2000), and these together with simultaneous recordings of underwater sounds, have been used to describe contextual sound production (Whitehead et al, 2000). For example, signals produced by cetaceans are used in maintenance of group cohesion (e.g. bottlenose dolphin, *Tursiops truncatus*, signature whistles produced during isolation to maintain contact between group members, Caldwell & Caldwell, 1965; Janik & Slater, 1998), in feeding contexts (e.g., bottlenose dolphin bray calls and humpback whale, *Megaptera novaeangliae*, trumpet-like feeding calls used in prey manipulation, Jurasz & Jurasz, 1979; Janik, 2000a; Sharpe, 2001), and in reproduction contexts (e.g., humpback whale song, Payne & McVay, 1971).

Despite the insights gained from such studies, visual observations are generally restricted to surface behaviour, which greatly decreases the amount of information available on individual or group behaviour. However, in recent years, electronic tags that can provide information on the underwater behaviour of study animals have been developed. Recent advances in electronic tag technology have increased the range of sensors that can be included, and multi-sensor tags are now regularly used to study a wide range of cetacean species (Johnson et al., 2009). Tags that simultaneously record sound, movement and orientation of the tagged animal provide detailed information on the individual behavioural context during sound production and help to elucidate the function of acoustic signals (Johnson & Tyack, 2003). For example, sound and movement recording tags have revealed that sperm whales (*Physeter macrocephalus*) use rapid-click buzzes called creaks during foraging, particularly during the bottom phase of foraging dives, where feeding is presumably occurring (Miller et al., 2004a).

Relating sound production to diving behaviour can be crucial to an understanding of how animals use the water column. For example, despite engaging in a similar diving behaviour, sperm whales and pilot whales (*Globicephala melas*) foraged during both deep and shallow dives, indicated by the production of foraging-related acoustic signals, while Blainville's beaked whales (*Mesoplodon densirostris*) foraged only during deep dives (Johnson et al., 2009). Sperm whales show clear patterns of

differential sound production as a function of depth. While clicks with varying inter-click intervals are mainly produced at depth, and are thought to be used in echolocation (Whitehead & Weilgart, 1990; Wahlberg, 2002), stereotyped sequences of clicks called codas are produced nearer to the surface and are thought to be used in inter-group communication (Watkins, 1977).

Killer whales are distributed worldwide and feed on a variety of prey species (Hoyt, 1994). However, different populations specialise in particular prey species and employ quite different group and individual behaviours depending on the prey they feed upon (e.g., intentional stranding: Lopez & Lopez, 1985; Guinet, 1991; Hoelzel, 1991; wave-washes: Visser et al., 2008). In Norway and Iceland, killer whales feed mostly on Atlantic herring (*Clupea harengus*). Here, killer whales have been described to use carousel feeding, a complex behaviour during which they herd the herring into a tight ball near the surface by swimming under and around the school in a highly coordinated manner, and then use tail slaps to stun the herring and eat the stunned fish one by one (Similä & Ugarte, 1993; Domenici et al., 2000; Simon et al., 2005). During carousel feeding killer whales are highly vocal, suggesting that sounds may be used to help herd the fish or coordinate the group's movements (Similä & Ugarte, 1993; Simon et al., 2007). Carousel feeding was first described in Norway and observations in Icelandic herring overwintering grounds in the 1980s suggested Icelandic killer whales also used carousel feeding (Sigurjónsson et al., 1988; Similä & Ugarte, 1993).

Other potential feeding behaviours of herring-eating killer whales have been little studied and most information comes from long-term studies conducted in herring overwintering grounds in Norway. Here, killer whales appear to perform deep dives (up to 160-180 m) to herd herring from deeper waters towards the surface, possibly using acoustic stimuli (Nøttestad & Similä, 2001; Nøttestad et al., 2002). Bringing the fish towards the surface allows whales to use visual stimuli in herding the prey, by flashing the white ventral side towards the fish school, to spend less energy, by performing shallower dives, and to use the surface as a barrier preventing the prey from escaping (Similä, 1997; Nøttestad & Similä, 2001). Indeed, most feeding behaviour appears to occur at relatively shallow depths (Similä, 1997). Apart from carousel feeding, individual killer whales engage in travel-feeding and subsurface feeding (Similä, 1997). Unlike carousel feeding, subsurface feeding does not involve bringing the herring school to the surface, but instead occurs underwater and only fish

scales and pieces were observed at the surface. It usually involves fewer whales, with less coordinated movements and less time around the herring school than carousel feeding (Similä, 1997).

Acoustic and movement recording tags (Dtags; Johnson & Tyack, 2003) attached to killer whales in Norway showed that periods of tail slapping were associated with highly circuitous movement, which were assumed to represent carousel feeding events. During these events, vocal activity increased and biphonic calls (2-component calls) were produced more often than during non-tail slapping periods (Shapiro, 2008). These findings supported the hypothesis that killer whales use biphonic calls, which may provide orientation cues (Miller, 2002; Miller et al., 2007), to aid in maintaining coordination between group members during carousel feeding. Tail slapping periods were either preceded by a suggested corralling period, during which calling activity was also high, movement was also non-directional but no tailslaps were produced, or a travelling period, during which the whales were silent (Shapiro, 2008).

Tailslaps are frequently recorded from killer whales in a herring spawning ground in Iceland (Simon et al., 2005, 2006). However, the feeding behaviour of these animals is little understood. Killer whales at this location are also more vocal during feeding (Simon et al., 2007) and additionally produce a 'herding' call, which appears to be used to manipulate prey, helping herd the herring into a tighter school to increase the success of a tail slap (Simon et al., 2006). During spawning, herring schools are considerably less dense and more dispersed than during overwintering (Nøttestad et al., 1996). However, no detailed studies have been conducted on the feeding behaviour of killer whales in spawning grounds, where the prey behaviour is likely to be very different from overwintering grounds (Nøttestad et al., 1996).

This chapter explores the diving and movement behaviour of killer whales in a herring spawning ground in Iceland and relates it to their vocal and tail slapping behaviour. It compares results with previous studies in Norwegian herring overwintering grounds to help understand how the feeding behaviour of killer whales may adapt to the different prey behaviours.

Methods

Study site

This study was conducted in Vestmannaeyjar in July 2009. Vestmannaeyjar is an archipelago off Southwest Iceland and a known spawning ground of the Icelandic Summer-Spawning (ISS) herring stock (see Chapter 3 for details of study area). Killer whales are regularly observed feeding on herring in this area during the summer months. Water depth in the study area was generally less than 100 m.

Diving behaviour

To investigate the natural diving behaviour of individual killer whales, digital archival tags (Dtags; Johnson & Tyack, 2003) were attached to whales with a suction-cups using a 7 m carbon fibre pole. The tags emit a VHF signal that allows the tagged whale to be tracked after deployment. Whenever possible, the tagged whale was followed for the entire duration of the deployment from a 9.45 m (31 feet) motorboat (Sandvik 945), using a VHF beacon and visual observations. Photographs of each tagged whale were collected for photo-identification. Individuals were identified based on the size and shape of the dorsal fin, the presence of nicks and scars, saddle patch pattern and body scars. Furthermore, each tagged whale was classified as adult male, adult female, juvenile or calf based on morphological characteristics (body size and size and shape of the dorsal fin), since the year of birth was unknown.

The tags have a pressure sensor sampling at a rate of 50 Hz, later down-sampled to 5 Hz. Pressure data were converted to depth in meters (with an accuracy of 0.5 m between 0 and 2000 m; Johnson & Tyack, 2003) using calibrated values. The tags also recorded sound and movements using two hydrophones and sampling at 96 kHz or 192 kHz, and three-axis magnetometers and accelerometers sampling at 50 Hz, which were later down-sampled to 10 Hz. Movement data was subsequently calibrated to provide the heading of the whale (Johnson & Tyack, 2003; Miller et al., 2004b).

The minimum depth of the tag when the whale surfaced depended on its position on the whale's body. Photographs of the tag's position on the whale's body were used to identify what minimum depth values were plausible. Dives were identified using a depth threshold based on the minimum depth thought to represent a surfacing. Each dive profile was checked to ensure no dives were missed; whenever there was a

question if the whale had surfaced or not, the acoustic record was checked to make a decision (Miller et al., 2010).

Only one study on diving behaviour of killer whales in this area had been conducted before (Schorr et al., 2001). Schorr et al. (2001) deployed 8 time-depth recorders (TDR) on killer whales off Vestmannaeyjar between 1999-2000. The diving behaviour of tagged whales in the present study was compared to the daytime diving behaviour previously reported by Schorr et al. (2001). For comparative purposes, the following dive parameters were calculated for all dives ≥1 min for all tag deployments: average number of dives/h (dive rate), average dive duration and the average number of dives/h at different depth bins. To further understand how tagged whales used the water column, the time spent at ≤10 m and the cumulative depth use was calculated for each whale, following the approach of Miller et al. (2010).

Calling behaviour during diving

The acoustic record of each tag was inspected using Adobe Audition 2.0© (Blackmann-Harris window; FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; 100% window width) and the beginning and end time of each acoustic signal that was detected was marked. Each sound was assigned a quality: 1) poor, when a contour was hardly seen in the spectrogram and sometimes only the sound was heard; 2) moderate, when a contour was seen but it was incomplete; and 3) good, when the full contour was clearly seen in the spectrogram (high quality). Calls of quality 3 were assumed to have been produced by the tagged whale or by whales in the immediate vicinity of the tagged whale and therefore at similar depths. Calls of lower qualities were likely produced by whales further away, and these were excluded from the analyses. The same criterion was used for high frequency whistles and tailslaps, therefore, only sounds of quality 3 were considered. No high quality herding calls were detected in the tag deployments, therefore all herding calls were removed from further analysis.

In this section I explore whether certain sound types occurred more often during different types of dives. Inspection of the dive profiles of tagged whales suggested that diving occurred as bouts of shallow dives followed by bouts of deep diving. To investigate if the diving behaviour could be divided using bout criteria, I conducted a log frequency analysis (Sibly et al., 1990) of maximum dive depth. Once the bout criterion for maximum depth was estimated, dives were classified into shallow or

deep dives. The number of high quality calls, high frequency whistles and tailslaps recorded in each dive type was calculated and compared between dive types.

Depth of sound production

To evaluate the depth at which sounds were produced only high quality sounds of three sound categories were considered: burst-pulse calls, divided into single-component (monophonic) and two-component (biphonic) calls; high frequency whistles; and tailslaps. The depth of the tagged whale at the time high quality sounds were recorded was extracted from the pressure sensor record to estimate the depth at which sounds had been produced. To examine variation in the depth of sound production, the number of high quality sounds in each depth bin (from 0 to 95 m at intervals of 5 m, i.e. 0-5, 5-10,…90-95 m) was calculated for each tag deployment. The median number of high quality sounds in each depth class was compared using a non-parametric Kruskal-Wallis test. If the number of groups k being compared is more than 5, as in this analysis, the Kruskal-Wallis test statistic H can be considered approximated by the χ^2 distribution with k-1 degrees of freedom (Zar, 1984). If sample sizes for a sound category did not allow for such a comparison, the depth distribution was inspected using a plot of the number of sounds in each depth class.

Heading features

To investigate if production of sound categories was associated with higher levels of circuitous movement, the heading data for each tag deployment were inspected. Higher circuitous movement should reflect a time period of increased angular deviation, because the heading angle changes more than during time periods of directional movement. The heading data of each tag deployment was divided into j time intervals of 5 min duration and the angular deviation (s_j) of the heading angle was calculated for each j time interval as (Zar, 1984):

$$s_j = \frac{180°}{\pi}\sqrt{2(1-r_j)}$$

where r_j (known as Rayleigh's statistic) varies between 0 and 1 and is a measure of concentration of the n angles in the chosen time interval. It is defined as:

$$r_j = \sqrt{\left(\frac{\sum_{i=1}^{n} \cos a_i}{n}\right)^2 + \left(\frac{\sum_{i=1}^{n} \sin a_i}{n}\right)^2}$$

The angular deviation can range from 0, when $r = 1$, to a maximum of 81.03°, when $r = 0$ (Zar, 1984). The number of high quality biphonic and monophonic calls, high frequency whistles and tailslaps in each time interval across all tag deployments was calculated.

Several time interval durations were tested (ranging between 5 s and 30 min) and histograms of the distribution of angular deviations were plotted for each time interval. Periods of non-directional movement should be characterised by high angular deviations while periods of directional movement should be reflected by low angular deviations. Therefore a time interval that best represented these two types of movement should be represented by a bimodal distribution of angular deviations. Figure 5.1 shows the distribution of angular deviations for the chosen time interval of 5 minutes, which best approached a bimodal distribution.

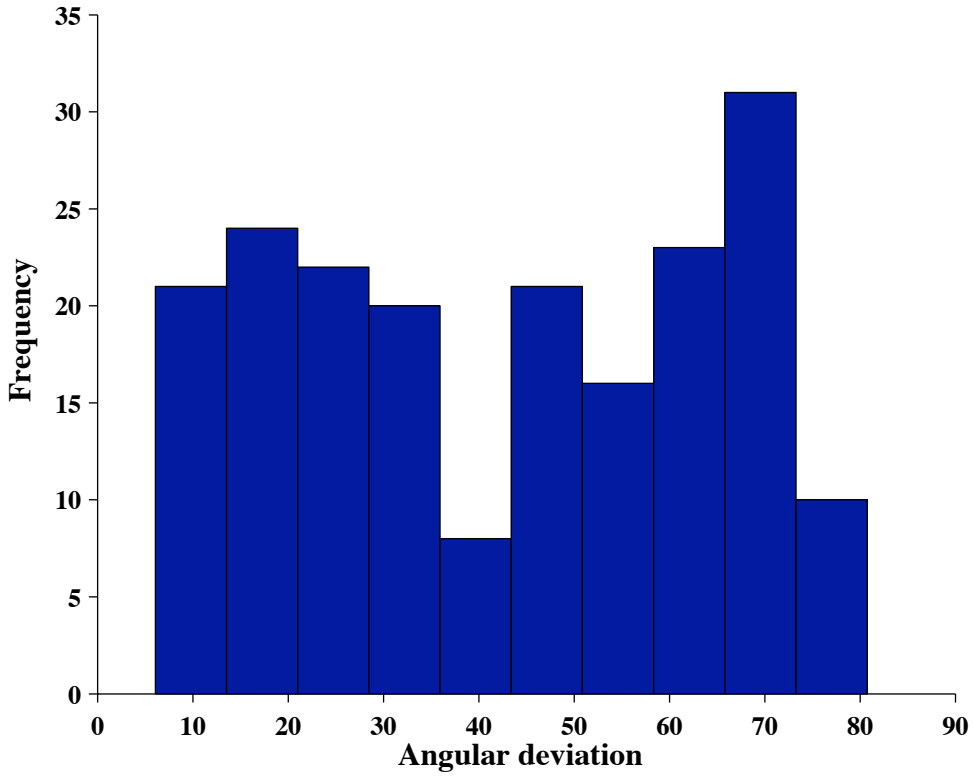

Figure 5.1. Distribution of angular deviations across all tag deployments using a time interval of 5 minutes.

To investigate the deviation in heading angles during tail slapping periods, only tag deployments that included high quality tailslaps were included. Data from all tags were included to see if calling increased during periods of increased deviation in heading angles. However, only tag deployments that included more than five calls of each type (monophonic and biphonic) were included in the comparison of the angular deviation of heading during periods of calling. Similarly, only tags with more than five high frequency whistles were included in comparisons between periods of high frequency whistle production and periods with no high frequency whistle production.

For a general overview of how the vocal and tail slapping behaviour related to the depth and movement measures, the pseudo-track of each tag deployment was generated and plotted. The pseudo-track is a non-georeferenced track of the tagged animal produced by dead-reckoning using the heading and pitch data, assuming a constant whale swimming speed and no water current (Johnson & Tyack, 2003). These plots included only quality 3 calls and high frequency whistles. I assumed tailslaps of quality 3 were produced by the tagged animal, while quality 2 tailslaps were probably produced by other animals in the same group. However, it is possible that some quality 2 tailslaps were produced by animals in other groups.

Results

Four Dtags were deployed in 2009, with deployment duration varying between 1.6 h and 6.5 h (Table 5.1). No strong reactions to tagging or change in general behavioural state were recorded, therefore the tag records are assumed to be representative of the tagged whale's natural behaviour. The Dtag deployment with the shortest duration was also the one registering the shallowest maximum dive depth. Therefore, this deployment may not accurately represent the full range of killer whale behaviours.

Table 5.1. Summary of tag deployments with information on date, name and duration of deployment, age/sex class of tagged individual, maximum depth reached during tag deployment and percentage of time spent at 10 or less meters during the whole tag deployment.

Date (dd/mm/yyyy)	Tag ID	Deployment duration (h)	Age/Sex class	Maximum depth (m)	% time at ≤10m
13/07/2010	oo09_194a	4.3	Juvenile	90.3	89
19/07/2010	oo09_200a	6.5	Unknown	77.1	64
20/07/2010	oo09_201a	4.2	Large juvenile	64.0	72
28/07/2010	oo09_209a	1.6	Adult female	33.9	59

Diving behaviour

The maximum depth of a dive was 90.3 m, but, on average, 71 ± 13 % (range: 59-89%; Table 5.1) of time was spent in the top 10 m of the water column. This is very similar to the value of 76% (range: 57-96 %) obtained by Schorr et al. (2001). To further compare the use of the water column between the animals tagged in this study and those of Schorr et al. (2001) study, dive parameters of dives ≥1 min were calculated for each of the tag deployments (Table 5.2).

Table 5.2. Dive parameters for dives ≥1 min from each tag deployed in this study. Rows 6-26 m, 26-50 m, 50-76 m and 76-100 m represent dive rates (number of dives/h) in those depth bins.

	oo09_194a	**oo09_200a**	**oo09_201a**	**oo09_209a**
Dives/h	16.14	10.67	13.50	14.09
Average duration (min)	1.59	2.84	2.10	2.92
6-26 m	7.95	4.79	11.4	12.81
26-50 m	0.70	3.40	1.19	1.28
50-76 m	0.23	1.70	0.47	0
76-100 m	1.17	0.15	0	0
Prop. dives ≥1 min	19 %	12 %	14 %	23 %

The dive rate (number of dives/h) and the average duration of dives varied slightly across all tag deployments but use of the 6-26 m depth bin was consistently higher, with a higher dive rate than any other depth bin (Table 5.2). The variation in dive rate and duration of dives is likely related to the behavioural context of the tagged animals during the deployments. In general, a higher dive rate was seen in deployments with a lower average duration (Table 5.2), which is consistent with more dives being made but of shorter duration during the same amount of time. However, less than 25% of the total number of dives in all tag deployments were longer than 1 minute (Table 5.2). This suggests that killer whales in this area mainly make short duration dives, probably to shallow depths.

Table 5.3 presents a comparison between the average dive parameters across all tag deployments in this study and those estimated by Schorr et al. (2001).

Table 5.3. Comparison between average dive parameters (for dives ≥1 min) across tag deployments in this study and those estimated by Schorr et al. (2001) from daytime data (presented in Simon et al., 2009). Rows 6-26 m, 26-50 m, 50-76 m and 76-100 m represent dive rates (number of dives/h) in those depth bins.

	Schorr *et al*. (2001)	**this study**
Average dives/h	9.2 (2.16)	13.6 (2.26)
Average duration (min)	2.4 (0.7)	2.4 (0.6)
6-26 m	1.6	9.2
26-50 m	1.8	1.6
50-76 m	3.6	0.6
76-100 m	0.36	0.33

The killer whales in this study seem to have a higher overall dive rate, as well as a higher dive rate between 6-26 m, than those tagged by Schorr et al. (2001). This difference could be due to different behavioural contexts of the whales tagged in the two studies. Additionally, the daytime data of Schorr et al. (2001) were based on only 5.5 hr of tag deployment (Simon et al., 2009) compared to the total of 16.6 hr of this study. It could therefore have been biased towards one behavioural state, such as foraging, during which animals may be easier to tag. It is possible that the longer tag deployments in this study were more representative of the variability in the dive behaviour.

Finally, Figure 5.2 illustrates the variation in time spent at different depths between tag deployments in this study. While only approximately 10% of the time is spent deeper than 10 m in tag oo09_194a, this proportion goes up to approximately 40% in tag oo09_209. Nevertheless, across all tag deployments most of the time is spent in the upper 10 m of the water column.

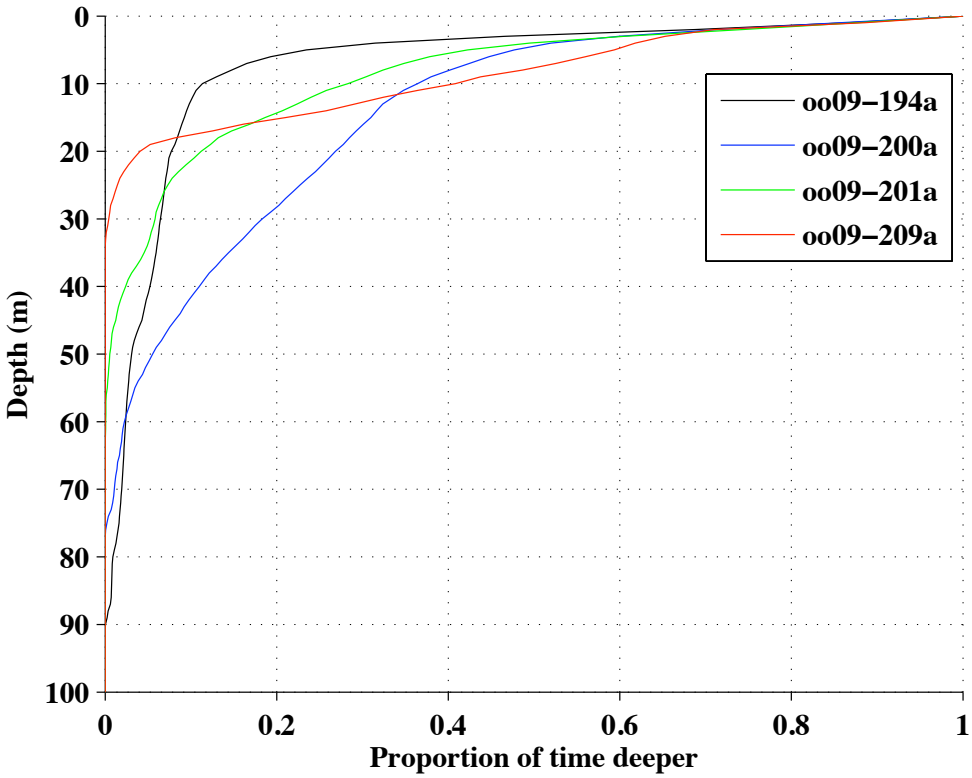

Figure 5.2. Proportion of time spent below a specified depth for each tagged whale.

Calling behaviour during diving

The log-frequency analysis suggested that dives could be separated into shallow and deep dives (Figure 5.3). A comparison between a single process model and a two processes model supported the use of the two processes model as a better fit for these data ($F_{[1,17]} = 47.9$, $p < 0.001$; Sibly et al., 1990). The bout criterion to separate shallow dives from deep dives that minimized the number of misassigned events (Slater & Lester, 1982) was 14.4 m. Therefore all dives with maximum depth ≥ 14.4 m were classified as deep dives, while all dives with maximum depth < 14.4 m were classified as shallow dives. From the total dives recorded across all tags, 7% were deep dives while 93% were classified as shallow dives. The tagged whales spent 64% of their time in shallow dives, and 36% of their time in deep dives.

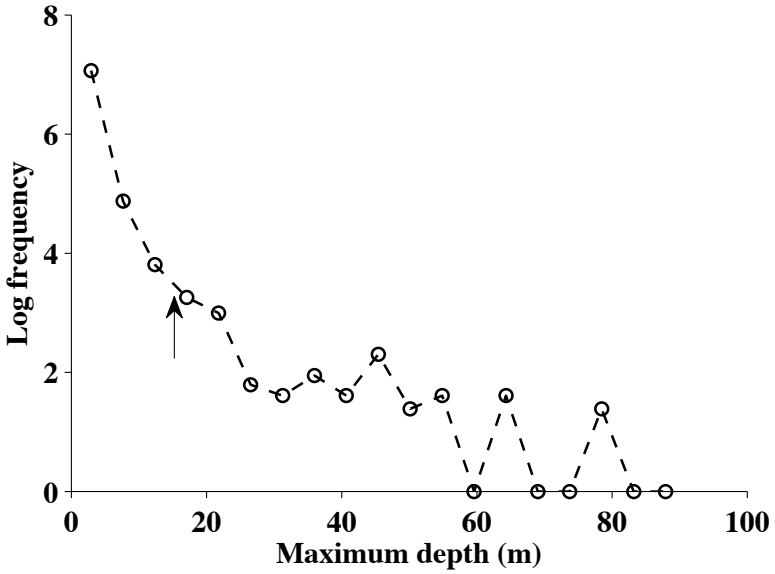

Figure 5.3. Log-frequency analysis of the maximum depth of dives. The arrow indicates the estimated bout-criterion.

All tailslaps (*n*=6) were recorded during deep dives. In contrast, the great majority (85.2%) of high frequency whistles (*n*=61) were produced during shallow dives. Burst-pulse calls (*n*=1170) showed a more balanced distribution. Most (57.9%) monophonic calls (*n*=1036) were produced in shallow dives, but this represented just over half of the sounds produced, while the remaining 42.1% were produced in deep dives. Similarly, 58.2% of biphonic calls (*n*=134) were produced during shallow dives and 41.8% were produced in deep dives.

Depth of sound production

Only quality 3 sounds were used to investigate the depth at which sounds were produced, regardless of the dive type they were produced in. A total of 1170 calls, of which 1036 were classified as monophonic and 134 were classified as biphonic, were identified across all tag deployments. Sixty-one high frequency whistles were identified, but only six tailslaps were identified. All tailslaps were recorded in the same tag deployment (oo09_200a). Figure 5.4 shows the distribution of the number of sounds produced at different depth classes.

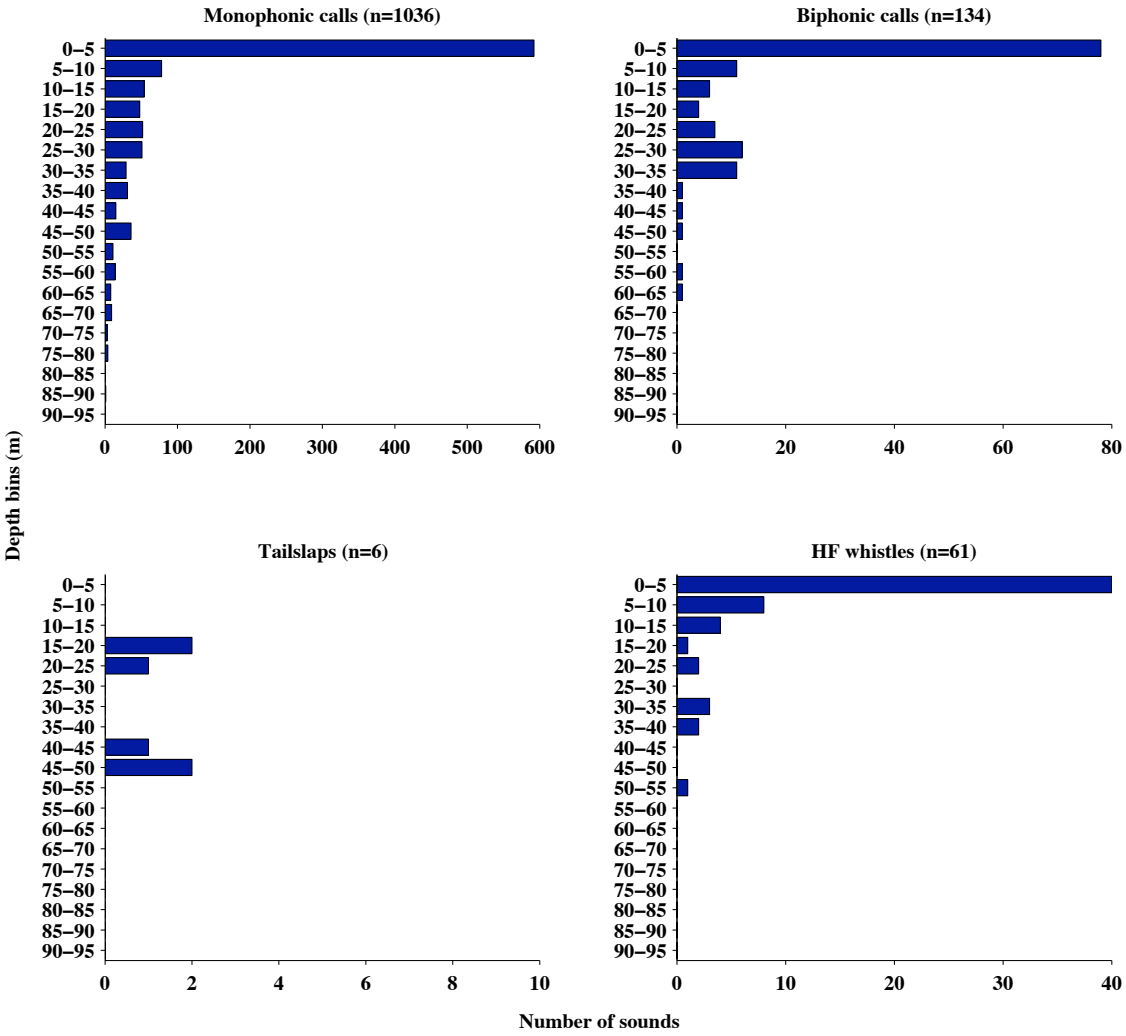

Figure 5.4. Depth of high quality calls, high frequency whistles (HF whistles) and tailslaps recorded across all tag deployments. Sample sizes for each sound type are shown in brackets. Note that all 6 tailslaps were recorded on tag deployment oo09_200a.

Most of the monophonic calls were produced in the top 5 m of the water column with a significant difference in the occurrence of monophonic calls at different depths (Kruskal-Wallis statistic=52.04, df=18, p<0.001). Biphonic calls had a very similar distribution, although the sample size is much smaller. In contrast, no tailslaps were recorded in the top 10 m of the water column, but there were peaks at 15-25 and 40-50 m depth, however the sample size was too small to test for differences across depth bins. Similar to the pattern observed with calls, high frequency whistles were mostly produced in the top 5 m of the water column and showed a significant difference in occurrence across depths (Kruskal-Wallis statistic=31.72, df=18, p=0.02). However, this occurrence of sounds at different depths may just be related to the time spent at

those depths. To correct for this, a histogram was created for of the number of sounds recorded per minute of time spent in each depth bin (Figure 5.5).

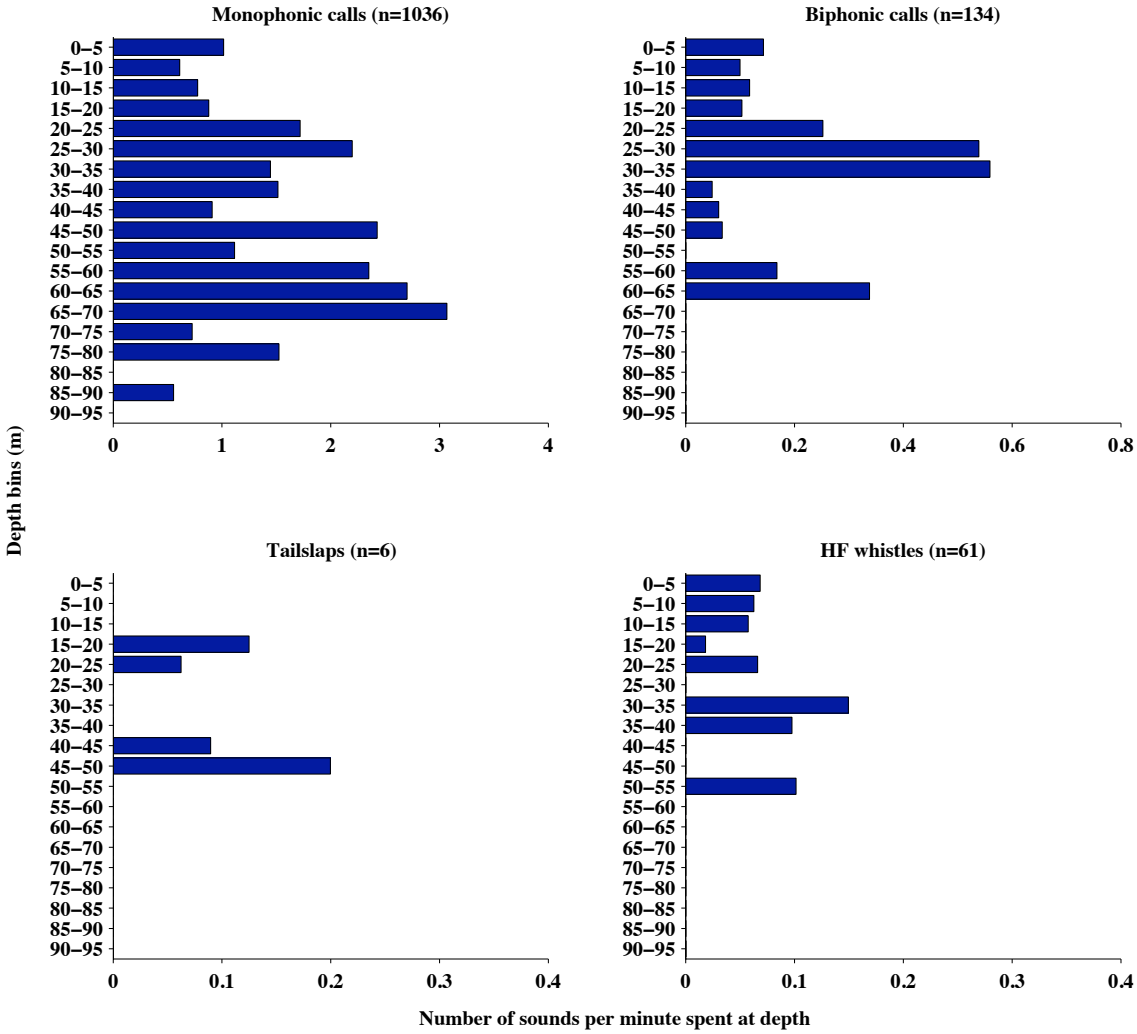

Figure 5.5. Rate of production of high quality calls, high frequency whistles (HF whistles) and tailslaps per minute spent at depth. Only tag deployments where sounds were recorded were taken into account to calculate the time spent at depth for each sound type. Sample sizes for each sound type are shown in brackets. All 6 tailslaps were recorded on tag deployment oo09_200a. Note that the x-axis values vary from panel to panel.

Once the time spent at depth is considered it is clear that monophonic calls present a more evenly distribution, with slightly higher rates at depths of 20-40 m and deeper than 45 m. Indeed, there was no significant difference in occurrence of monophonic calls across depth bins (Kruskal-Wallis statistic=18; df=18; p=0.46). High frequency whistles also seem more evenly distributed, and there was no significant difference in occurrence of high frequency whistles across depth (Kruskal-Wallis statistic=14.42; df=11; p=0.21).

The depth distributions of different sound types were then compared using Kolmogorov-Smirnov tests. The rate of monophonic call production differed significantly from that of biphonic calls (Kolmogorov-Smirnov test statistic=0.84; $p<0.001$), high frequency whistles (Kolmogorov-Smirnov test statistic=0.89; $p<0.001$) and tailslaps (Kolmogorov-Smirnov test statistic=0.89; $p<0.001$).

Heading features

Figure 5.6 compares the angular deviation in periods of production of each sound class with periods when no sounds of that type were recorded.

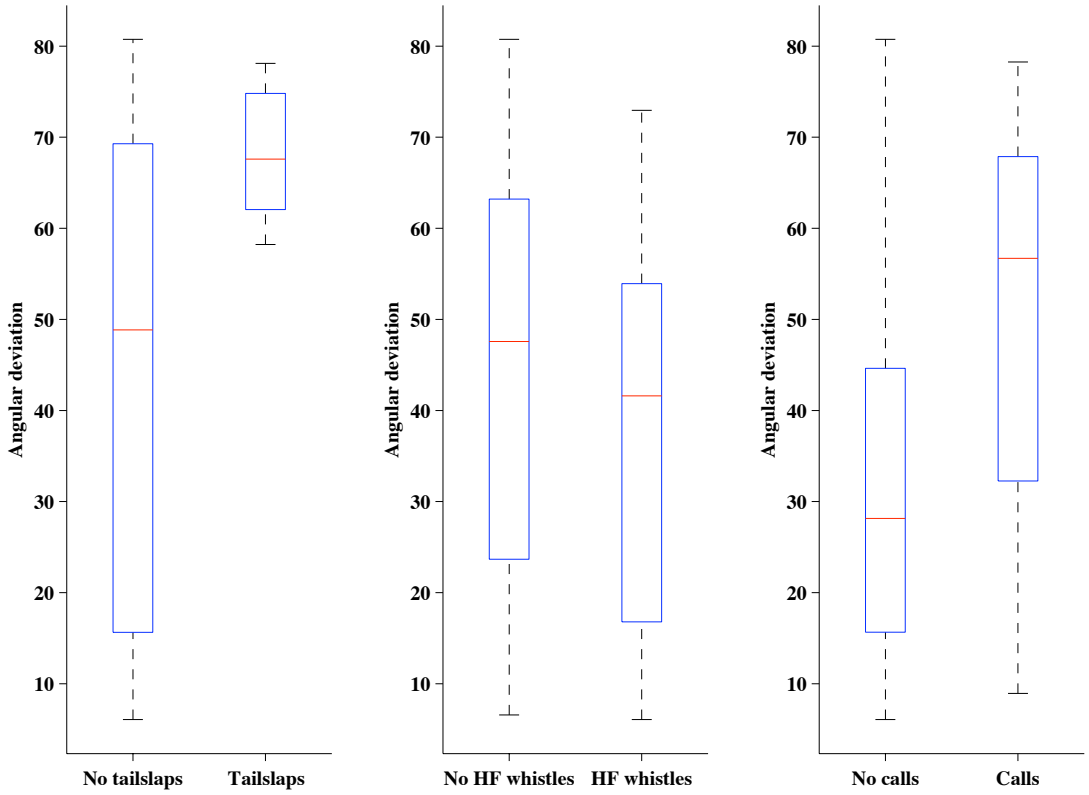

Figure 5.6. Distribution of angular deviation for time intervals with no sounds and time intervals with sounds. Note that the distribution for tailslaps contains only data from tag oo09_200a. The distribution of high frequency whistles (HF whistles) includes all tags except oo09_209a. The distribution for calls includes all tag deployments.

The distribution of angular deviation during periods of no tail slapping for tag oo09_200a is wide, as it includes periods with both directional movement and non-directional movement where no high quality tailslaps are recorded. However, tailslaps were only produced during time periods with high angular deviations (Figure 5.6).

This is the only tag deployment included for tailslap production as this was the only one where high quality tailslaps were recorded.

In contrast, high frequency whistles seem to be more common during periods with slightly lower angular deviations, or periods of straighter directional travel. Finally, periods of call production tended to occur at higher angular deviations than periods of no call production.

Figure 5.7 shows the distribution of angular deviations during periods of no call production (*n*=28 5-min periods), periods of production of only monophonic calls (*n*=20 5-min periods) and periods where both monophonic and biphonic calls were produced (*n*=29 5-min periods). Because tag oo09_200a was the only record with more than five calls of each type, only this one deployment was included. None of the 5-min time intervals in this tag deployment contained only biphonic calls, therefore this category was not plotted. Periods with both monophonic and biphonic calls occurred only at high angular deviations, while periods of production of only monophonic calls occurred over a wide range of angular deviations. Periods with no call production tended to occur at low angular deviations.

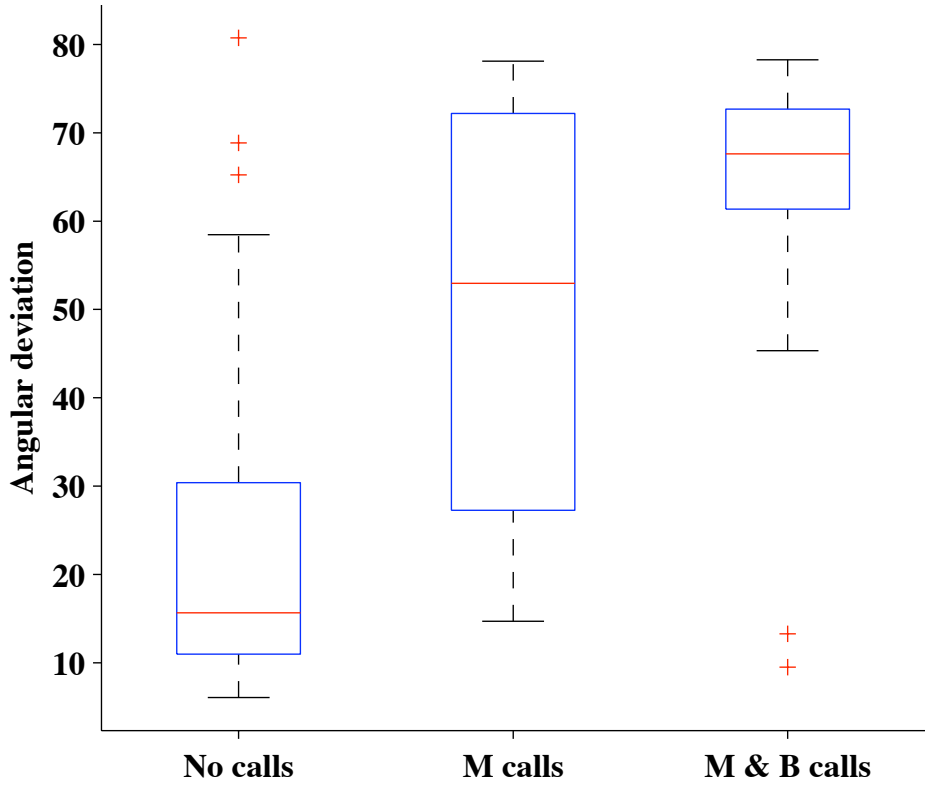

Figure 5.7. Distribution of angular deviation of tag oo09_200a during time intervals with no calls in comparison with time intervals with monophonic calls only (M calls) and time intervals with both monophonic and biphonic calls (M & B calls).

The pseudotrack plots for each tag deployment are presented in Figures 5.8 to 5.11. These plots allowed for each tag deployment to be analysed more carefully with respect to the relationship between diving, movement behaviour and sound production.

Figure 5.8 shows the pseudotrack of tag oo09_194a. In general this deployment is characterised by short periods of directional movement, where production of calls appears to occur in bouts, but these bouts occur both during periods of shallow diving and deep diving. Only two tailslaps, both of quality 2, were detected during this deployment, and these could have been from whales other than the tagged whale's group. Nevertheless, both tailslaps occurred during periods of call production and in one case during a period of deep diving. Most high frequency whistles were produced during periods of calling, while the animals was undertaking shallow diving and relatively directional movement.

Figure 5.9 displays the pseudotrack of tag oo09_200a. This is the longest deployment with a total duration of 6.5 hr. It starts with a period of directional movement with slight turns, during which the whale was mostly silent and performing shallow diving. Only a few high frequency whistles were produced during this period. At the end of this period, some calls were produced just before the animal executed a sharp turn and started a period of non-directional movement, which lasted for approximately 4.5 hr. This period of highly circuitous movement was characterised by deep dives and increased calling. All tailslaps and biphonic calls were produced during this period, as well as some high frequency whistles. Nevertheless, most of the calls produced in this period were monophonic.

Figure 5.10 displays the pseudotrack of tag oo09_201a. This deployment started with a short period of non-directional movement during which tailslaps, monophonic and biphonic calls were recorded. Only tailslaps of quality 2 were detected and dives were relatively shallow. The remainder of the deployment was characterised by short periods of relatively directional movement during which calling appeared to occur in bouts. High frequency whistles were only produced during periods when calls were also produced. Towards the end of the deployment deeper dives, characterised by increased calling, including biphonic calls, and production of high frequency whistles occurred but movement was relatively directional.

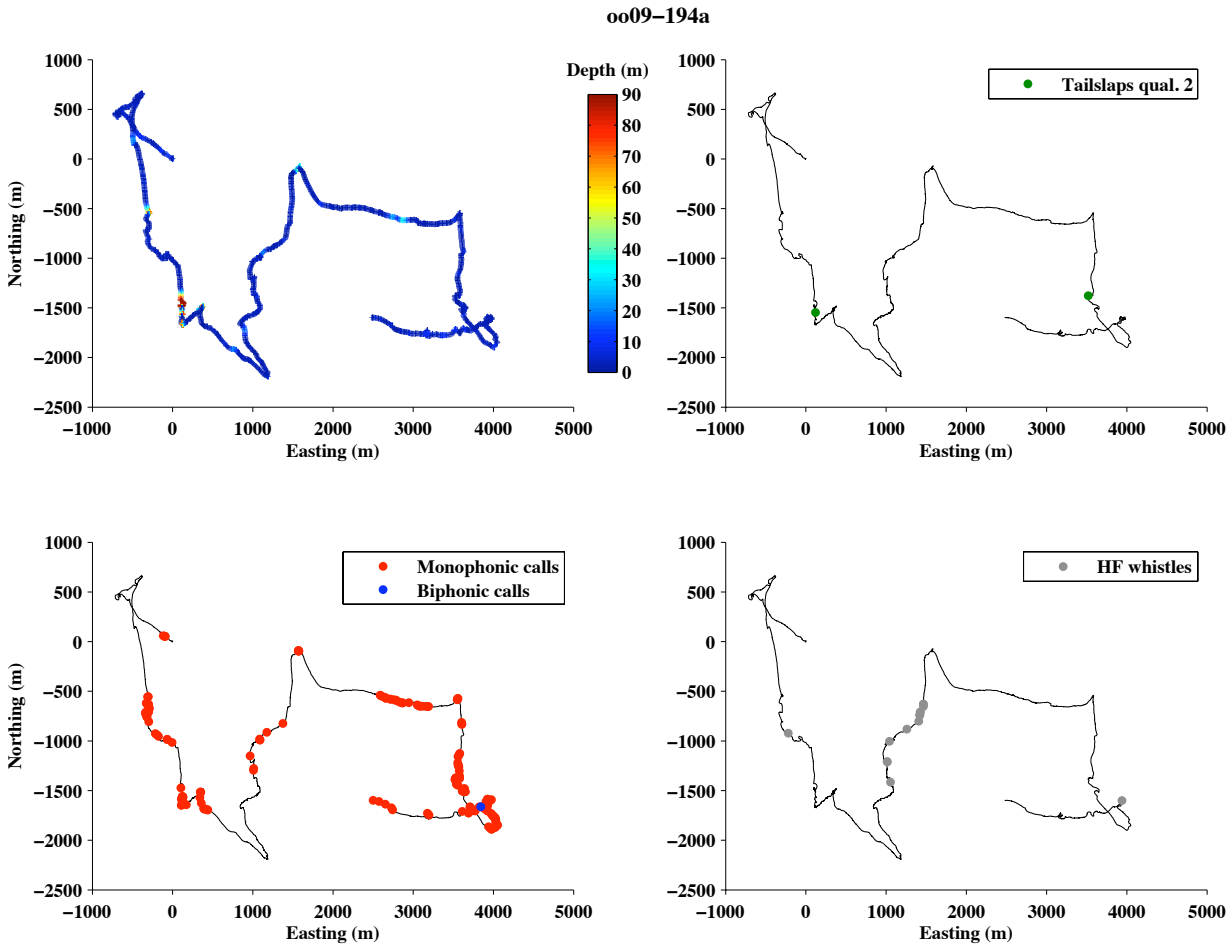

Figure 5.8. Pseudotrack (non-georeferenced) of tag oo09_194a, showing horizontal movement as relative distance and direction since the tag was deployed (point 0-0). The top left plot shows dive depth in colour. Only tailslaps of quality 2 (medium quality) are shown since no quality 3 (high quality) were recorded. All other sound categories displayed include high quality sounds only.

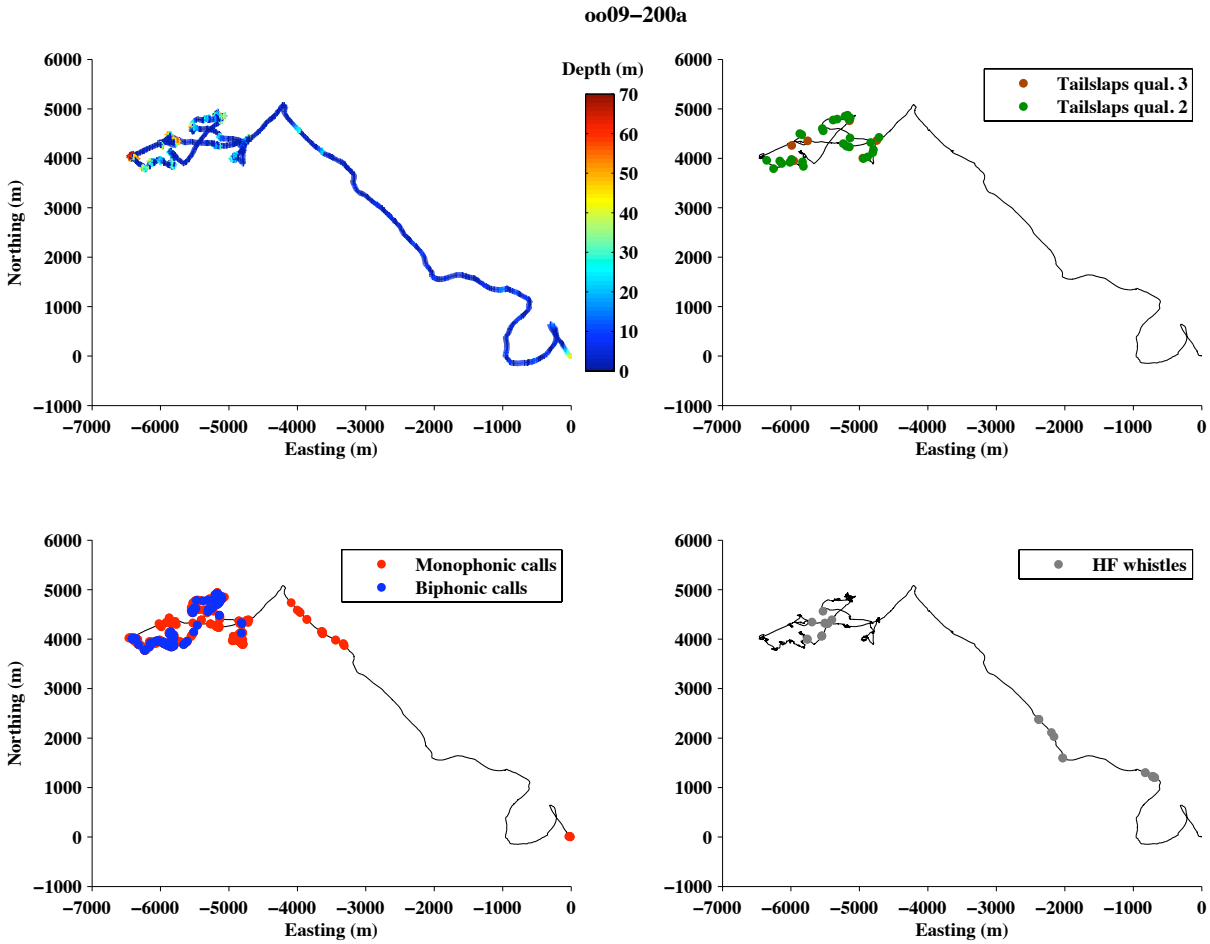

Figure 5.9. Pseudotrack (non-georeferenced) of tag oo09_200a, showing horizontal movement as relative distance and direction since the tag was deployed (point 0-0). The top left plot displays dive depth in colour. Tailslaps are distinguished between quality 3 (high quality) and quality 2 (medium quality). All other sound categories displayed include high quality sounds only.

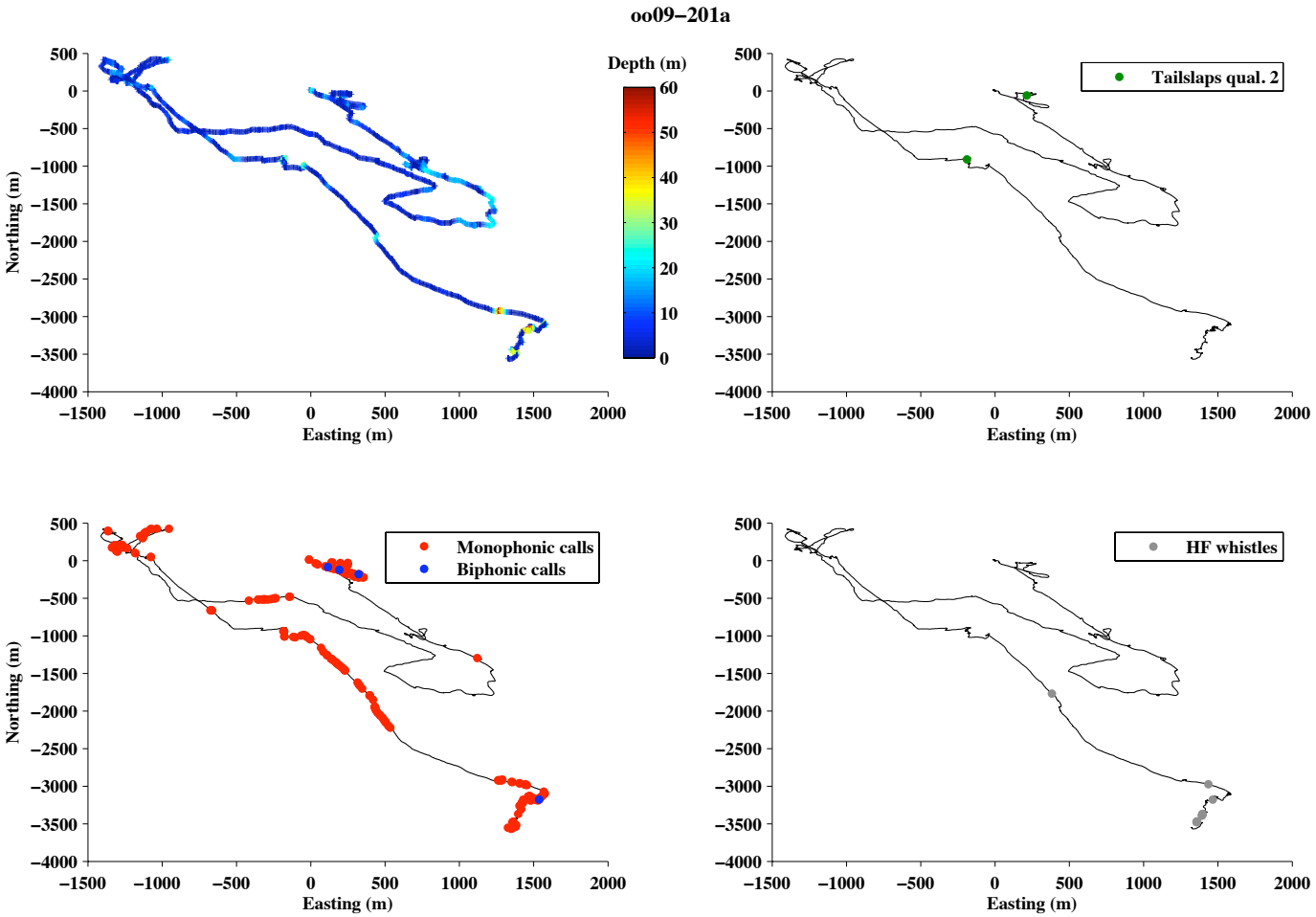

Figure 5.10. Pseudotrack (non-georeferenced) of tag oo09_201a, showing horizontal movement as relative distance and direction since the tag was deployed (point 0-0). The top left plot displays dive depth in colour. Only tailslaps of quality 2 (medium quality) are shown since no quality 3 (high quality) were recorded. All other sound categories displayed include high quality sounds only.

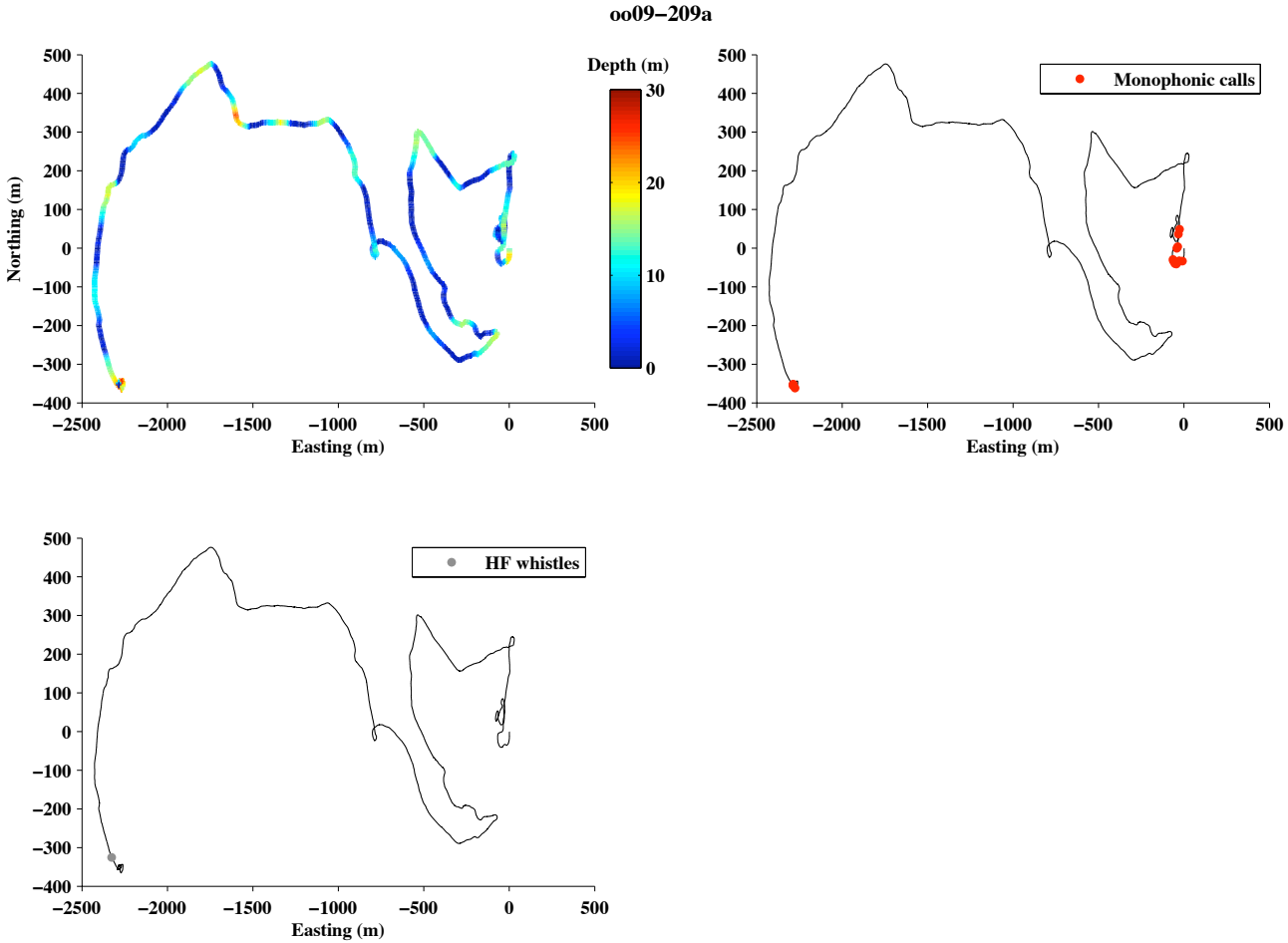

Figure 5.11. Pseudotrack (non-georeferenced) of tag oo09_209a, showing horizontal movement as relative distance and direction since the tag was deployed (point 0-0). The top left plot displays dive depth in colour. All sound categories displayed include high quality sounds only.

Figure 5.11 displays the pseudotrack of tag oo09_209a. This is a short deployment (1.6 hrs) characterised by short periods of relatively directional movement generally with shallow dives. There was little sound production during this deployment. A few monophonic calls were recorded in the beginning of the deployment and the whales then remained silent until the end of the deployment when one high frequency whistle and one monophonic call were recorded.

Discussion

Killer whales in this study spent the majority of their time in the top 10 m of the water column. This is a common feature of killer whale diving behaviour across different populations (e.g., Baird et al., 2005; Miller et al., 2010). The deepest dive recorded was to 90.3 m. Nevertheless, as pointed out by Schorr et al. (2001), the depth of killer whale dives in this area is most likely limited by the bottom topography, because water depth rarely exceeds 100 m. The use of the water column, however, varied between tag deployments, probably reflecting the different behavioural contexts of tagged whales.

Periods of deep diving were generally characterized by the presence of tailslaps, increased calling and non-directional movement. In fact, tailslaps were only recorded during deep dives. Tailslaps are used during foraging (Similä & Ugarte, 1993; Simon et al., 2005), which suggests that periods of deep diving were related to foraging. Although the whales spent the majority of their time in the top 10 m of the water column, tailslaps were always recorded when whales were at deeper depths. Although only one of the tag deployments included tailslaps of quality 3, the depth distribution of these tailslaps generally agreed with the distribution found previously using another dataset (Chapter 4). The depth estimates of tailslap production found here are slightly deeper than depths previously reported for killer whales carousel feeding in Norway, where the estimated depth of tailslaps was between 0-10 m (Simon et al., 2005). Similä (1997) reports a tailslap between 1-20 m depth from subsurface feeding killer whales in Norway, but mentions that in observations of killer whales interacting with herring schools at 50-100 m depth no tailslaps were observed. Tailslaps recorded by Shapiro (2008) using Dtags were also mainly produced in the top 20 m of the water column. The effectiveness of tailslaps may be strongly related to depth (Nøttestad & Similä, 2001), therefore it is likely that killer whales use these most commonly in shallower waters.

This difference in depth of tailslaps between this study and those conducted elsewhere could be due to the fact that killer whales feeding on overwintering herring presumably drive the herring up from deeper waters and feeding occurs mainly at the sea surface. The depths at which tailslaps are produced likely reflects the depth of the prey. In the spawning ground, where this study was conducted, killer whales have never been observed feeding at the surface, with herring jumping out of the water, as seen in herring overwintering grounds. This supports the hypothesis that the herring prey is found deeper and feeding occurs at greater depths. It is possible that the whales in this area are using a feeding behaviour more similar to the sub-surface feeding described in Norway, which also does not involve bringing the fish to the surface (Similä, 1997). This feeding behaviour involved less coordination among whales, smaller groups and few tailslaps. Tailslaps are regularly recorded from killer whales feeding in the Vestamanneyjar study area (Simon et al., 2005, 2006; Chapter 4), therefore the feeding behaviour used may be somewhat different from sub-surface feeding. Additionally, many of the feeding events were observed near small seamounts. This could have reflected the location of the prey or could be because killer whales used the topography at these sites to aid in trapping the prey.

Although the production of certain types of sounds, like tailslaps, was related to diving and movement features, other sound types seemed to be produced during a range of movement and diving patterns. Monophonic calls were produced equally often during shallow and deep dives, although tagged whales spent most of the time in shallow dives. Most calls were produced in the top 5 m of the water column. This is not surprising, given that killer whales spend the majority of their time at these depths. Indeed, when calling rates were corrected for the time spent at depth, the rate clearly increased quite strongly with depth. This suggests that monophonic calls have a relevant function during periods of feeding at depth. However, production of monophonic calls also occurs during periods of directional movement that do not appear to be related to feeding. It is possible that the tag deployments also captured events of socialising, during which the whales produced monophonic calls.

Most high frequency whistles were also produced during bouts of calling, but mostly during shallow dives. When corrected for time spent at depth, the rate of high frequency whistle production increased with depth but this was based on only a few whistles that were recorded during deep dives. These sounds were produced during periods of presumed feeding and during periods of more directional movement. This

provides an unclear picture of the usage of high frequency whistles. The fact that the sample size considered here is relatively small (61 high quality whistles from four tag deployments) makes inferences about their possible functions difficult.

In contrast, biphonic calls appear to be produced primarily during periods of non-directional movement, when tailslaps also occurred. These were presumed to be periods of feeding. Biphonic calls appear to be produced equally often during deep and shallow dives, although most of the time was spent in shallow dives. The calls were also mostly recorded in the top 5 m of the water column. However, when corrected for the time spent at different depths, the calling rate increased with depth, particularly at similar depths to those where tailslaps also occurred. This suggests that biphonic calls are particularly relevant during feeding and may be used to coordinate foraging behaviours, as suggested by Shapiro (2008). The directionality cues that are inherent in biphonic calls (Miller, 2002) may be particularly important during coordinated foraging that includes high levels of direction changes.

Nevertheless, the overall proportion of biphonic calls produced (11%) is much smaller than that of monophonic calls. Biphonic calls represented 19% of all the calls produced during the feeding period characterised by circular movements and tailslaps in deployment oo09_200a, where most (n=129) of the biphonic calls were recorded. This is a smaller proportion than the proportion of biphonic calls observed during tail slapping periods in most tag deployments in Norway (range: 16-56% and four out of seven deployments > 30%; Shapiro, 2008). This may simply be a consequence of the relatively small sample size in the present study, but it may suggest that the feeding strategies employed for spawning herring may require less coordination than carousel feeding, and consequently less production of orientation cues. This would suggest that killer whales in this study use a feeding strategy that is similar to sub-surface feeding (Similä, 1997).

The movement of killer whales in this study was characterised by periods of highly non-directional movement, which also included deep dives, the production of biphonic calls and tailslaps. These movement and sound production features are characteristic of feeding killer whales in Norway (Shapiro, 2008), which suggests that these periods in Iceland were most likely related to feeding. However, deep dives were generally associated with periods of feeding. Previous studies conducted in this area showed that killer whales regularly dive close to or to the bottom of the seafloor, at depths between 40 and 100 m (Schorr et al., 2001). It is likely that many of the

deep dives recorded in this study were also to the seafloor, due to the shallow depths in the area and varying topography. During the spawning stage of their life cycle, herring schools generally settle on the bottom, move along irregular tracks and are less dense than before or after the spawning stage (Nøttestad et al., 1996). This prey behaviour is consistent with the observations of feeding taking place in deeper waters.

Analysis of the movements of each tagged whale indicated overall erratic tracks (Figures 5.8-5.11). As mentioned above, the movements of spawning herring schools are more irregular than before or after spawning (Nøttestad et al., 1996). This may explain why the movements of killer whales were also generally irregular, as killer whales may have been attempting to locate herring schools.

This study suggests that killer whales adopt different foraging strategies when feeding on spawning herring than when feeding on overwintering herring. This implies that the prey behaviour influences the feeding behaviour of these predators, as would be predicted. Feeding on spawning herring seems to take place at greater depths, which could be because the benefits gained by bringing the fish to the surface do not outweigh the costs spent doing so. It is possible that spawning herring schools are less dense and smaller than overwintering schools, which may increase the difficulty of maintaining a herring ball for a prolonged period of time. There may not be enough fish to justify the involvement of a large group of whales trying to encircle one herring school. This, in turn, suggests that the feeding strategies used would require less coordination between group members. The relatively low production of biphonic calls, thought to aid in coordination during carousel feeding between group members (Shapiro, 2008), observed here supports this conclusion.

Corralling appears to precede some of the carousel feeding events in Norwegian overwintering grounds. This behaviour is characterised by highly non-directional movement and increased calling, but no production of tailslaps (Shapiro, 2008). Such behaviour was not observed in this dataset. Periods of non-directional movement are characterised by deep dives and production of tailslaps and therefore seem highly related to feeding periods. This suggests the whales are not spending considerable time periods diving deep to corral herring from deeper waters before feeding takes place, as suggested in overwintering grounds. Additionally, killer whales seem to travel in erratic movements, possibly searching for herring schools. This, again, could be because the herring school density is lower. Unlike overwintering grounds where killer whales seem to break up smaller schools from large herring aggregations in

deep waters (Nøttestad et al., 2002), the widespread distribution of spawning herring may not justify such corralling behaviour.

Although this study points to some differences in feeding behaviour between Iceland and Norway, the tag deployments used here were relatively short (maximum of 6.5 hours), so that the full diversity of natural behaviours may not be accurately represented. Certainly, only a few presumed feeding events were observed. For example, no high quality herding calls were detected during these tag deployments, yet these are known to be relevant sounds during feeding, at least on some occasions (Simon et al., 2006). In the future, more tag deployments and for longer periods would aid in the study of the foraging strategies of killer whales in a spawning ground and the function of acoustic signals produced. In addition, deploying multiple tags in the same group would allow for investigations of the role of different group members (e.g., Shapiro, 2008) or different age/sex classes (e.g., Miller et al. 2010). Finally, integrating studies on the behaviour of killer whales with information on the herring behaviour would allow for a more detailed investigation of the causes of variation in killer whale feeding strategies.

Chapter 6

General Discussion

In this thesis, I have sought to explore the possible function of calling in herring feeding killer whales. Studying a species' sound production in defined social and behavioural contexts allows researchers to formulate hypotheses about the potential functions of different signals in a repertoire. Observational studies provide baseline information about the contexts in which communication occurs (e.g., Whitehead et al., 2000). The study of signal design characteristics will also provide an understanding of the variability in the repertoire of a given species. In this study I attempted to explore possible functions of sounds produced by herring-eating killer whales by investigating design characteristics of the different signals they produced and contextual sound production.

Killer whales are the marine mammal with the widest geographic distribution, and their acoustic signalling and behaviour patterns have been described in many studies, and yet we still know little about the function of the acoustic signals produced by this species. Vocal behaviour seems to be related to the prey species killer whales feed upon and the associated costs when sounds produced may be detected by their prey (Barrett-Lennard et al., 1996; Deecke et al., 2005). Fish-eating populations vocalise quite extensively and produce a variety of sounds thought to be used for communication. However, understanding the function of these sounds is made difficult by our inability to directly observe interactions between individuals and receivers' responses to emitted signals.

Studies across different locations have shown that killer whales can exhibit a variety of behaviours, with some of the variation apparently dependent upon the prey species that compose their diet. In fact, almost every population studied to date has been described to use a different strategy to capture their prey. In some cases, foraging behaviours are shared across two or more locations. For example, tailslaps are used by killer whales in Norway, Iceland and the Northwest Pacific to feed on schooling prey (Simon et al., 2005; Tarasyan et al., 2005). Other behavioural variants appear to be unique to one population. For example, only killer whales in the

Antarctic are known to use wave-washes to force their prey into the water (Visser et al., 2008). This behavioural plasticity possibly reflects adaptations to the environment and diversity of prey behaviour.

In the Northeast Atlantic our understanding of killer whale behaviour is still in its infancy, compared to the long-term datasets that exist elsewhere. Nevertheless, the differences found to date have supported the argument that killer whales in this region should form a separate ecotype (Simon et al., 2007). In Norway and Iceland killer whales feed primarily on the Norwegian spring-spawning (NSS) and Icelandic summer-spawning (ISS) stocks of Atlantic herring (*Clupea harengus*), respectively (Sigurjónsson et al., 1988; Stenersen & Similä, 2004; Simon et al., 2007). In Norway killer whales appear to follow the NSS herring stock migration (Stenersen & Similä, 2004) but less is known about the Icelandic killer whale population's movements. Killer whales in Iceland and Norway exhibit similarities in vocal behaviour (Simon et al., 2007), foraging behaviour (Sigurjónsson et al., 1988; Similä & Ugarte, 1993) and are closely genetically related (Morin et al., 2010; Foote et al., 2009b). Despite previous suggestions that these whales may have been in contact in the past, due to the overlapping migration areas of herring stocks they preyed upon (Jonsgård & Lyshoel 1970; Jakobsson & Østvedt 1999), comparisons of killer whales photo-identified since the 1980's in Iceland and Norway did not find any matches (Sigurjónsson et al. 1988; Foote et al. 2009b).

This study set out to contribute to our understanding of the function of sounds produced by herring-eating killer whales, by investigating signal design features and contextual sound production. I first described a newly-discovered signal, the high frequency whistle, and investigated the whistle repertoire of different herring-eating killer whale populations. I investigated signal design features of this signal, as well as the most commonly produced burst-pulse calls, to test different hypotheses on signal function. Finally, the environmental and behavioural contexts of sound production were investigated. The results were compared with previous studies of herring-eating killer whales in Norway, as well as fish-eating killer whales elsewhere.

Sound repertoires

Comparative studies of delphinid whistles have shown that the interspecific variation in frequency parameters is higher than intraspecific variation. Interspecific variation in whistle maximum frequency is particularly correlated with body size,

suggesting that the larger the delphinid body size the lower the maximum frequency of whistle it produces (Ding et al., 1995; Matthews et al., 1999; Podos et al., 2002). Killer whales are the largest delphinid and therefore a particularly interesting species to study to understand the relationship between body size and whistle frequency parameters.

Although killer whales are one of the best-studied cetacean species, all of the information on the species' whistle frequency parameters came from studies done with resident killer whales in the coastal waters of British Columbia, Canada. This lack of studies of killer whale whistles is undoubtedly due to the fact that, unlike other delphinids, whistles are not the most common sound produced by killer whales (Ford, 1989). Most of the studies on killer whale acoustic communication have focused on the burst-pulse calls, the most common sound produced (Ford, 1989).

Resident killer whale whistles were shown to be somewhat different from other delphinid whistles, being longer and more complex, and most likely functioning in close-range communication during socialising (Ford, 1989; Thomsen et al., 2002). Whistle fundamental frequencies were thought to be restricted to the human audible range (Thomsen et al., 2001). In Chapter 2 I investigated the production of whistles in the ultrasonic frequency range by killer whales.

Using wide-band acoustic sampling recordings I showed that killer whales produce whistles with the highest fundamental frequency ever reported in a delphinid. This supported previous arguments that whistle maximum frequency was not constrained by body size (May-Collado et al., 2007b). However, production of these high frequency whistles was not widespread across different populations. High frequency whistles were detected in three populations in the Northeast Atlantic but not in two populations in the Northeast Pacific, suggesting substantial intraspecific variation in killer whale whistle repertoires. These differences in the whistle repertoire between the Northeast Pacific populations and the Northeast Atlantic populations supports a classification of the Northeast Atlantic populations into a separate ecotype (Simon et al., 2007) but do not clarify what function these signals may have.

I compared the high-frequency whistle repertoires of the populations in the Northeast Atlantic and showed that whistles were short duration signals, with simple contours (with few inflection points) and that most had entirely ultrasonic fundamental frequency contours reaching a maximum of 75 kHz. Although there

were some differences in whistle maximum frequency and frequency range between Iceland and Norway, overall most methods were not able to distinguish between whistles produced in the two locations. This suggested that high frequency whistle repertoires of killer whales from different locations in the Northeast Atlantic are very similar.

High frequency whistles described here are markedly different from the previously known lower frequency killer whale whistles. Unlike the long and complex low frequency whistles produced by killer whales (Thomsen et al. 2001), high frequency whistles are short and simple and may therefore encode different information. Unlike the differences in whistle repertoires found between northern and southern resident killer whales (Riesch et al., 2006), high frequency whistles appear to be very similar between different populations. The low complexity of high frequency whistle contours and the similarities across different populations suggest that these whistles do not encode individual, group or even population information. Delphinid signals containing such group or individual specificity appear to encode such information in the frequency contour (Janik, 2006; Riesch et al., 2006), therefore if high frequency whistles had a similar function higher contour variation would have been expected.

Although this study described a new signal that to date has only been detected in the Northeast Atlantic, it is too premature to assume this same signal is not produced by any other populations elsewhere. Further wide-band acoustic recordings from other populations would help us understand if the production of these sounds is somehow related to unique features of the social lives of Northeast Atlantic populations in particular. For this, recordings will require a sampling rate of at least 192 kHz, as it is possible that only whistles entirely above 48 kHz are produced.

The observed differences in the use of high-frequency whistles by killer whales in the Atlantic and Pacific ocean basins did not reflect general prey preferences, as fish-eating killer whales were sampled in both cases, or genetic differentiation, as resident killer whales appear to be more closely related to herring-eating killer whales than to transients (Morin et al., 2010). Investigations of the behavioural context of whistle production in Chapter 5 also did not suggest that whistles were produced in behaviours specific to Northeast Atlantic killer whales. It is possible that the existence of high-frequency whistles in Northeast Atlantic killer whales reflects specific selective pressures on Northeast Atlantic killer whales, but further studies will be

necessary to explain the causes of the observed differences in whistle production. Nevertheless, this level of intraspecific variation appears to be unparalleled in delphinids, and highlights the importance of sampling several populations and using appropriate acoustic sampling techniques when deriving species parameters to be used in comparative analyses of sound repertoires.

The precise function of these sounds remains unknown, but the observational work in this thesis should help in forming hypotheses that can be examined in further work. Chapters 3 and 4 indicated that these are likely to be short-range signals that are produced across the water column, though at higher rates per unit time at depths >10m where feeding-related sounds were also localized. The acoustic features of the whistles do not appear to be strongly affected by pressure differences at the depths they were observed to produce high-frequency whistles. In Chapter 5 I showed that high frequency whistles were mostly produced during bouts of calling but both during presumed feeding and non-feeding events. This paints an unclear picture of what the function of these sounds may be, but their presence throughout most recording events suggests they do play a relevant role in the communication system of Northeast Atlantic killer whales. A larger sample of observations of behavioural context during high frequency whistle production would be helpful to propose details of possible functions. Nevertheless, given the signal characteristics described in this study it is likely that they function as short-range signals during social contexts.

Signal design – sound source levels and active space

In Chapter 3, I also investigated proposed functions of killer whale calls by estimating their source levels and active spaces. Because sound production by this killer whale population increases during feeding, particularly production of burst-pulse calls (Simon et al., 2007), calling had been suggested to help herd the fish or coordinate the groups' movements during active feeding (Similä & Ugarte, 1993; Simon et al., 2007). On the other hand, observations of groups joining previously feeding groups suggested that calling could also function to attract other conspecific groups to large feeding aggregations (Shapiro, 2008). These two proposed functions would likely select for different source levels and active spaces, either for signals to function over short ranges for within-group communication, or over longer ranges for between group communication.

This study showed that, in comparison to previously reported source levels of killer whale calls in British Columbia (Miller, 2006), calls produced by herring-eating killer whales in Iceland had relatively low source levels and were predicted to be short-range signals. A similar case of intraspecific variation in source levels has also been shown for bottlenose dolphins. While in the Moray Firth dolphins produced whistles with average source levels of 158 dB (Janik, 2000b), in Australia estimates of source levels averaged 147 dB (Jensen et al., 2011b). This occurred despite the increased background noise levels in Australia, indicating the dolphins were not compensating for the effects of noise (Jensen et al., 2011b). Although these differences in source level were not discussed in the context of differences in group spacing or behavioural context, it is possible that the lower source levels and active spaces reflect differences in the distances over which communication needs to occur to benefit the signaller.

The smaller estimated active space of killer whale calls in Iceland agreed with suggestions that calls are used for communication between group members within a feeding bout, which will generally be within short ranges of each other. However, it is possible that these source levels were related to the specific context of feeding on spawning herring and that signalling killer whales might benefit from producing higher source level sounds while feeding on overwintering herring. Only in herring overwintering grounds have killer whale groups been suggested to join other feeding groups and even possibly congregate in an area to cooperatively herd herring from deep waters (Nøttestad et al., 2002; Shapiro, 2008). In the herring spawning ground where this study was conducted, large aggregations of feeding whales were encountered but different groups did not appear to be working together to cooperatively feed on the same school of herring. This difference in behaviour may be related to the prey behaviour. It is possible that in contexts in which it is advantageous to advertise a feeding patch to other groups that may join to help herd a large school of herring, call source levels will be higher than those reported here. Estimating source levels of killer whale calls produced in a herring overwintering ground, particularly during observations of joining feeding groups would be very helpful to resolve this question.

Killer whales appear to adjust the source levels of calls with changing environmental noise conditions (Holt et al., 2009) and it is possible that source levels are also adjusted depending on behavioural context and the need to attract conspecific

groups located at greater distances. Future studies of call source levels and estimated active spaces should monitor spacing between groups and between members of the same group, as well as behaviour context.

Contextual sound production

Killer whales make use of the water column in their daily lives and the way they utilize this environment is likely related to the prey they feed upon (Baird et al., 2005; Miller et al., 2010). Sound production at depth may affect the characteristics of signals produced, as has been shown in other species (e.g., Ridgway et al., 2001). However, little is known about how sound production relates to this use of the water column. Particularly in herring-eating killer whales, that are known to produce most sounds during feeding (Simon et al., 2006), the depths at which sounds are produced and what effects these may have on sound production are relatively unexplored. Because killer whales appear to have resonant structures that provide cues to the sex of a signaller (Miller et al., 2007) sounds produced at different depths might be expected to differ with increasing pressure. In Chapter 4 I investigated the depth of sound production of different sound types and the characteristics of sounds produced at different depths.

The finding that no effects of depth were apparent in any of the sound parameters tested suggested that, at least in the depth ranges attained by the whales studied here, signals will not suffer major effects of increasing pressure. This may simply be a result of the shallow depths that killer whales in the area regularly dived to not being sufficient to cause clear effects on sound parameters. Indeed, other cetacean species that have shown effects of depth on their sound characteristics dived to much deeper depths than those studied here (Ridgway et al., 2001; Jensen et al., 2011a). Alternatively, killer whales could be somehow compensating for the effects of depth in their sound production mechanism. Whatever the reason, these findings indicated that information transmitted by the duration and frequency characteristics of the sound types studied here will remain reliable regardless of the depth of the signaller.

On the other hand, the depths at which sounds were produced varied across the localized sound type. While calls and high frequency whistles occurred across most depths, tailslaps and herding calls, which are feeding-related sounds, occurred only below 10 m. However, there were differences in the depth of localized tailslaps and herding calls. While tailslaps were produced up to 42 m depth, herding calls were

only produced in shallower depths, primarily from 10-25m depth. The small sample size may have biased these results nevertheless it is possible that herding calls are associated with particular feeding strategies that are only used in shallow waters. I suggest that killer whales feeding on spawning herring use foraging strategies different from carousel feeding, which generally takes place at the surface, because the depths at which feeding seems to occur were deeper than 10 m. The fact that calls and high frequency whistles were also detected at these depths suggested production and function of these sounds may also be relevant during active feeding events. However, this analysis lacked a correction for the time spent at depth by killer whales in this area as well as an understanding of the behavioural context in which the different sounds are produced.

A correction for time spent at depth to derive calling rates for depth layers was attempted in Chapter 5, where I investigated in more detail how the sound production related to the behaviour context of killer whales using data from animal-attached sound and movement recording tags. This study showed that, as previously described for this species, killer whales in this area spent most of their time diving to shallow depths (< 10 m). All sounds produced had higher rates of production at depths >10m where feeding was taking place (Chapter 5, Figure 5.3), as indicated by production of tailslaps at those depths.

Deeper diving was in general associated with highly non-directional movement, increased sound production and production of tailslaps, which suggested these were periods of feeding and that feeding took place at depths >10m. These periods were characterised by production of biphonic calls, which have higher source levels in resident killer whales (Miller, 2006) and have been suggested to aid in group coordination during carousel feeding (Shapiro, 2008). This suggested that calling, particularly production of biphonic calls, may be relevant during feeding, possibly as a means to aid in group coordination. In fact, some biphonic calls were produced at high source levels in this study, indicating that those types of sounds are within the repertoire of Icelandic herring-eating killer whales. Calling rates in tagged groups, particularly for the biphonic calls were found to increase during periods in which higher rates of turning were noted (Chapter 5, Figure 5.7). That could indicate that the directionality cues inherent in biphonic calls (Miller, 2002) are particularly important during coordinated foraging that includes high levels of direction changes. The lower rate of biphonic call production in comparison to that reported in

Norwegian overwintering herring grounds hints at less need to acoustically coordinate behaviour in spawning grounds than during complex carousel feeding. It also supports the conclusion that long-range communication was not as strongly favoured in killer whales feeding upon Icelandic spring spawning herring than may be the case when killer whales feed upon overwintering herring.

The focus of this thesis research was the acoustic behaviour of herring-eating killer whales, but this study suggests that the foraging strategies used when killer whales are feeding upon spawning herring may be an important factor in how they produce communication signals. The lack of published work with detailed observations of how killer whales are interacting with their prey makes it difficult to propose in detail what are the foraging strategies used by killer whales feeding upon spawning herring. A description of this behaviour would require more detailed data being collected on killer whale behaviour during feeding. However, a crucial piece of information that is lacking is the relationship between prey behaviour and predator foraging strategy. Killer whales, as a species, show a remarkable variety of foraging strategies depending on the prey they feed upon (e.g., Guinet, 1991; Visser et al., 2008). Optimal foraging theory predicts that animals should employ foraging strategies that maximise energy gain. It is possible that in a spawning ground, where the prey density is lower, large schools like those found in overwintering grounds do not exist and consequently highly coordinated behaviour to maintain a large school of herring near the surface is not required. The whales may adopt different strategies that allow them to exploit the smaller schools while minimising energy expenditure. Future studies should address this issue by simultaneously sampling the prey and predator behaviours to help understand what foraging strategies are used.

It is possible that some of the differences in foraging behaviour suggested here could be due to population-specific behaviours. Most studies conducted in the Northeast Atlantic have been based in the Norwegian herring overwintering grounds. Therefore, similar comparisons in Icelandic overwintering grounds would be beneficial. For example, herding calls have only been recorded in the spawning grounds in Iceland. It is possible that this call is only used during a foraging strategy employed in spawning grounds, due to the different prey behaviour. Alternatively, this call may be specific to certain groups that have only been recorded in the spawning grounds studied here. The lack of knowledge on group repertoires of Icelandic killer whales makes it impossible to answer such questions at present and

such information would be crucial for our better understanding of herring-eating killer whale behaviour.

This study has provided some insights into the sound production and behaviour of herring-eating killer whales. However, there are still unanswered questions that deserve further study. Northeast Atlantic killer whales show unique behaviours and acoustic signals that support their classification into a separate ecotype and therefore deserve continuing studies. The role of prey behaviour changes in the behaviour of killer whales is still little understood and this study suggests that within the same population feeding strategies may be flexible and change according to the behaviour of the prey. Future studies at different life stages of the prey would help us understand the flexibility in killer whale behaviour and how it may adapt to changing environmental conditions and prey behaviours.

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Appendix 1

Samarra *et al.*: JASA Express Letters [DOI: 10.1121/1.3462235] Published Online 19 October 2010

Killer whales (*Orcinus orca*) produce ultrasonic whistles

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Abstract: This study reports that killer whales, the largest dolphin, produce whistles with the highest fundamental frequencies ever reported in a delphinid. Using wide-band acoustic sampling from both animal-attached (Dtag) and remotely deployed hydrophone arrays, ultrasonic whistles were detected in three Northeast Atlantic populations but not in two Northeast Pacific populations. These results are inconsistent with analyses suggesting a correlation of maximum frequency of whistles with body size in delphinids, indicate substantial intraspecific variation in whistle production in killer whales, and highlight the importance of appropriate acoustic sampling techniques when conducting comparative analyses of sound repertoires.

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PACS numbers: 43.80.Ka [CM]
Date Received: May 7, 2010 **Date Accepted:** June 14, 2010

1. Introduction

Evolutionary studies of animal communication seek to identify selective pressures that influence signal design and variation. In delphinids, frequency parameters of tonal signals ("whistles") have low intraspecifc variation when compared to variation across species (e.g., Ding *et al.*, 1995). Body size has been suggested to explain interspecific variation as it is negatively correlated with whistle frequency (e.g., Ding *et al.*, 1995; Podos *et al.*, 2002), although once phylogeny is taken into account this relationship no longer holds for whistle maximum frequency (May-Collado *et al.*, 2007). However, measurements made to describe acoustic sig-

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nals are inherently constrained by acoustic sampling decisions. For example, an insufficient sampling frequency may result in whistles or parts of whistles being missed (e.g., Oswald *et al.*, 2004).

Killer whales are the largest delphinid and therefore particularly relevant to investigate the relationship between body size and whistle frequency. Although the harmonics of killer whale calls and whistles can extend well above 20 kHz (e.g., Miller, 2002), whistle fundamental frequencies have only been reported up to 16.7 kHz (Thomsen *et al.*, 2001). However, most studies of killer whale sound production have only investigated the frequency band audible to humans (up to 20 kHz). Here we use recordings with high sampling rates to demonstrate that killer whale whistles extend to ultrasonic frequencies (>20 kHz), but apparently only in certain populations.

2. Methods

Acoustic recordings were made off British Columbia, Alaska, Norway, Iceland and Shetland using a 96 kHz sampling rate. Only Northern Residents (fish-eating, Ford *et al.*, 1998) were recorded in British Columbia and only West Coast Transients (mammal-eating, Ford *et al.*, 1998) were recorded in Alaska. No effort was made to control the orientation or range of the whales to the recording devices. Recording systems varied between locations and included towed and vertical hydrophone arrays and sound recording tags attached using suction cups ["Dtags;" Johnson and Tyack, 2003; see Supplementary material for details on all recording systems]. A smaller sample of higher sampling frequency recordings was collected in Norway and Iceland using Dtags and a single hydrophone (see Supplementary material).

High frequency whistles were defined as tonal sounds with fundamental frequency contours entirely above 17 kHz, as this was the maximum frequency previously reported for killer whale whistles (Thomsen *et al.*, 2001). Although terminology used to refer to tonal sounds of short duration may vary between authors, here we have refrained from making such distinctions without further knowledge on the potential functions of whistles of varying durations. Recordings were inspected using Adobe Audition 2.0© (Blackmann-Harris window; FFT=2048 or 4096, for 96 kHz and 192 kHz sampling rates, respectively; 100% window width). Whistle contours entirely above 17 kHz and with sufficient signal to noise ratio were traced from visual inspection of the spectrogram using a peaks contour extraction algorithm (Buck and Tyack, 1993; Hann window; frequency resolution=46.875 Hz; time resolution=0.667 ms). From the extracted fundamental frequency contour we measured the following descriptive parameters: beginning, half-way point (mid) and end frequency, minimum and maximum frequency, frequency range (maximum-minimum frequency), duration and whistle complexity as zero, one or more inflection points (after Ding *et al.*, 1995).

3. Results and discussion

Killer whale whistles were found to extend into the ultrasonic frequency range with observed fundamental frequencies ranging up to 75 kHz (Fig. 1; Table 1), higher than previously described for any delphinid. However, high frequency whistles were only detected off Iceland, Norway and Shetland. High frequency whistles were detected in most encounters (Iceland =96%; Norway=73%; Shetland=100%; Supplementary material) and occurred during bouts of calling but represented on average only 6% (Norway, based on 14 Dtags), 10% (Iceland, based on 4 Dtags) and 2% (Shetland, based on 1 towed array recording) of communicative signals detected (pulsed calls, low and high frequency whistles). Most high frequency whistles detected had an entirely ultrasonic fundamental frequency contour (Iceland=97%; Norway=99%; Shetland =87.5%). On the smaller sample of Dtags sampling at 192 kHz some of the detected whistles had a fundamental frequency contour entirely above 48 kHz but these were usually less frequent than whistles in the 17–48 kHz band. In one Dtag record from Norway 2008, however, only whistles above 48 kHz were detected.

We can confidently ascribe these sounds to killer whales as no other cetaceans were observed during recordings of killer whales in Iceland, Norway or Shetland. Localization of

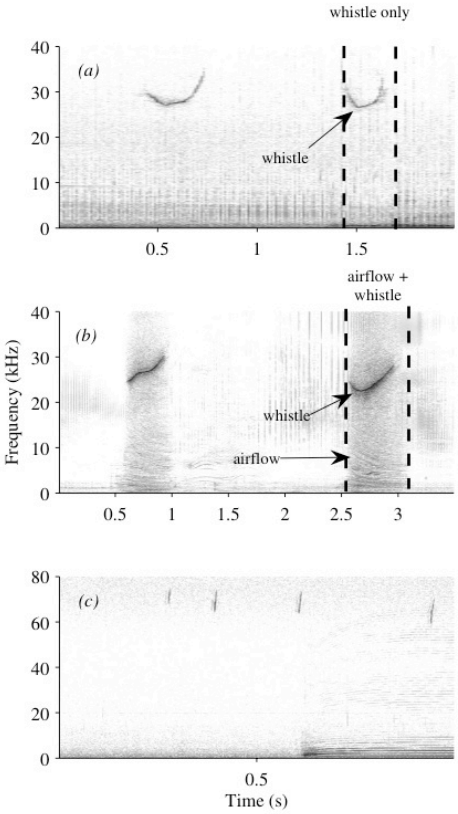

Fig. 1. Example spectrograms of ultrasonic whistles from Icelandic killer whales (*Orcinus orca*): (a) below 48 kHz; (b) below 48 kHz with overlapping airflow sound; (c) above 48 kHz. Note the presence of an airflow sound entirely overlapping the whistles in (b) but not in (a). In real time only the airflow is audible, but once slowed down both the ultrasonic whistles and the airflow sound are audible (see multimedia files Mm. 1.wav and Mm. 2.wav). Recordings (a) and (c) were sampled at 192 kHz, and (b) at 96 kHz. Spectrogram parameters: FFT size: (a) 4094, (b) 2048, (c) 1024; overlap: 50%; window function: Hann; frequency resolution: [(a) and (b)] 46.875 Hz, (c) 187.5 Hz; time resolution: [(a) and (b)] 10.67 ms, (c) 2.67 ms.

whistles with the vertical array resulted in short ranges, agreeing with visual observations of killer whale groups. Finally, air movement sounds clearly overlapped some intense whistles recorded by one Dtag deployed close to the blowhole [Fig. 1(b); Mm. 1 and Mm. 2]. Most of the energy of the airflow sound is in lower frequencies, and its frequency decreases through time, suggesting airflow into the nasal air sacs changes their resonant frequencies during whistle production. This likely artifact of whistle production indicates that those whistles were produced by the tagged animal. Further work should evaluate whether characteristics of the airflow sound itself might be used to study the sound-production mechanism of high frequency whistles.

Mm. 1. Recording made using an animal-attached sound recording tag (Dtag) sampling at 192 kHz and deployed close to the blowhole. This sound clip corresponds to the spectrogram presented in Fig. 1(b). An airflow sound is audible twice in this real time recording but not the coinciding ultrasonic whistles. Faint clicks and a call can also be heard in the background.

Table 1. Descriptive statistics (mean ± stdv and range given in parentheses) of high frequency whistle fundamental frequency contours recorded from killer whales off Iceland, Norway and Shetland. For Iceland and Norway whistles with fundamental frequencies entirely above 48 kHz are listed in separate rows. Sample sizes and the Nyquist frequency of recordings from which contours were measured are given in parentheses. Note that due to the small sample size from Shetland, descriptive statistics from this sample may not be representative.

	Beginning frequency (kHz)	Frequency at $\frac{1}{2}$-way point (kHz)	End frequency (kHz)	Minimum frequency (kHz)	Maximum frequency (kHz)	Frequency range (kHz)	Duration (s)	% with ≤1 inflection points
Iceland (n=548, 48 and 96 kHz)	31.3 ± 6.7 (16.9–47.3)	32.5 ± 5.8 (17.6–45.2)	37.0 ± 6.3 (19.4–50.5)	30.4 ± 5.9 (16.9–44.5)	37.2 ± 6.4 (19.4–50.5)	6.8 ± 3.7 (0.8–21.2)	0.14 ± 0.14 (0.008–0.81)	98
Norway (n=234, 48 and 96 kHz)	31.7 ± 6.1 (17.6–45.2)	32.1 ± 5.8 (19.0–42.8)	35.3 ± 6.4 (19.8–46.6)	30.7 ± 5.9 (17.4–42.3)	35.7 ± 6.0 (22.3–46.6)	5.0 ± 2.5 (1.0–19.9)	0.17 ± 0.30 (0.01–4.2)	97
Shetland (n=8, 48 kHz)	22.6 ± 2.1 (20.2–26.1)	23.6 ± 2.7 (21.3–29.3)	28.0 ± 3.4 (25.2–35.3)	22.2 ± 2.3 (19.9–25.9)	28.0 ± 3.4 (25.3–35.4)	5.8 ± 2.1 (3.5–9.5)	0.34 ± 0.13 (0.14–0.47)	88
Iceland >48 kHz (n=22, 96 kHz)	64.0 ± 2.7 (60.6–71.2)	65.9 ± 2.3 (58.1–68.8)	68.5 ± 3.2 (60.0–74.7)	63.1 ± 2.8 (55.6–68.3)	68.7 ± 3.0 (61.9–74.7)	5.6 ± 2.4 (0.7–10.4)	0.04 ± 0.07 (0.006–0.25)	95
Norway >48 kHz (n=23, 96 kHz)	64.3 ± 3.6 (56.6–71.0)	59.2 ± 3.3 (53.3–64.3)	58.1 ± 5.4 (47.1–68.3)	55.9 ± 4.0 (47.1–64.3)	65.1 ± 3.4 (57.9–71.0)	9.1 ± 4.1 (3.6–19.5)	0.04 ± 0.03 (0.02–0.14)	100

Mm. 2. The same recording as in Mm. 1 but slowed down six times. The airflow sounds become clearer and the ultrasonic whistles audible. Note that the airflow sound coincides with the whistles, suggesting it is an artifact of whistle production.

These results suggest that killer whales fall well outside the proposed relationship between body size and maximum whistle frequency (e.g., Ding *et al.*, 1995) and therefore reinforce the conclusion that maximum whistle frequency does not seem to be constrained by body size in this species group (May-Collado *et al.*, 2007). Interestingly, whistle maximum frequency appears to vary substantially across killer whale populations, in contrast to what is usually reported for delphinids (e.g., Ding *et al.*, 1995). Whistles from Northern Residents and West Coast Transients seem restricted to the audible frequency range, while whistles recorded off Iceland, Norway and Shetland are commonly produced in the ultrasonic range. As we had no recordings of Northern Residents or West Coast Transients at sampling rates higher than 96 kHz, we cannot rule-out the possibility that these whales also produce whistles entirely above 48 kHz. Nevertheless, as Icelandic and Norwegian killer whales have been suggested to form a separate ecotype due to their unique behavior (Simon *et al.*, 2007) they may be under different selective pressures, which may explain these differences in whistle production. Further research is necessary to clarify what factors drive such intraspecific variation in killer whales, nevertheless, it emphasizes the importance of sampling different populations to infer species' whistle frequency parameters used in comparative studies.

Killer whales have the best hearing sensitivity between 18 and 42 kHz with an upper hearing limit of roughly 100 kHz (Szymanski *et al.*, 1999). They therefore should be able to detect the whistles described here, although signal duration may affect absolute thresholds (Johnson, 1968). It remains unclear how killer whales detect and use high frequency whistles in their communication, yet the fact that these signals are recorded in most encounters suggests they are a relevant part of their communication system. Harmonics were present in 65 of 78 high frequency whistles recorded at 500 kHz sampling rate. Of these 65 whistles, only 22 had harmonic energy extending above 100 kHz, with 164 kHz being the maximum frequency of any harmonic. Relative levels of harmonics may provide information on the signaler's direction of movement (e.g., Miller, 2002), which could be important in cooperative contexts. The frequency characteristics of these signals suggest a use in short-range communication. However unlike the long and complex low frequency whistles (Thomsen *et al.*, 2001), high frequency whistles are short and simple (Table 1) and therefore may encode different information. As Icelandic and Norwegian killer whales are generally silent when traveling and call most intensively during feeding or socializing (Simon *et al.*, 2007) high frequency whistles, which are produced primarily during bouts of calling, are likely related to such contexts.

Acknowledgments

We would like to thank everyone involved in the fieldwork. Funding was provided by Carnegie Trust for the Universities of Scotland, Fisheries and Ocean Canada, Fundação para a Ciência e a Tecnologia studentship to F.I.P.S. (Grant No. SFRH/BD/30303/2006), Office of Naval Research, Royal Society, Russell Trust Award (U. St Andrews), Scottish Executive Environment and Rural Affairs Department, Scottish Natural Heritage, U. of Iceland, and U.S. National Oceanographic and Atmospheric Administration through the North Pacific Universities Marine Mammal Consortium, The National Geographic Society, The Vancouver Aquarium and Woods Hole Oceanographic Institute (WHOI) Ocean Ventures Fund and Rinehart Coastal Research Center. We would like to thank International Fund for Animal Welfare/The Song of the Whale Team, particularly C. Lacey, for providing recordings from Iceland 2004, WHOI, especially A. Bocconcelli, M. P. Johnson and P. L. Tyack for support with tagging projects and P. Madsen (U. of Aarhus) for lending a hydrophone and amplifier. The Dtag data from Norway 2005 was collected in collaboration with A. D. Shapiro. We thank F. Plard, A. Podt and M. Eggleston for their help with analysis of the Norway 2005, 2009 Dtag and Shetland data, respectively. Anonymous reviewers provided helpful comments. All field research was carried in compliance with local regulations.

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Appendix 2

This appendix shows the distribution of all measurements of parameters of the fundamental frequency contour of high frequency whistles recorded off Iceland and Norway.

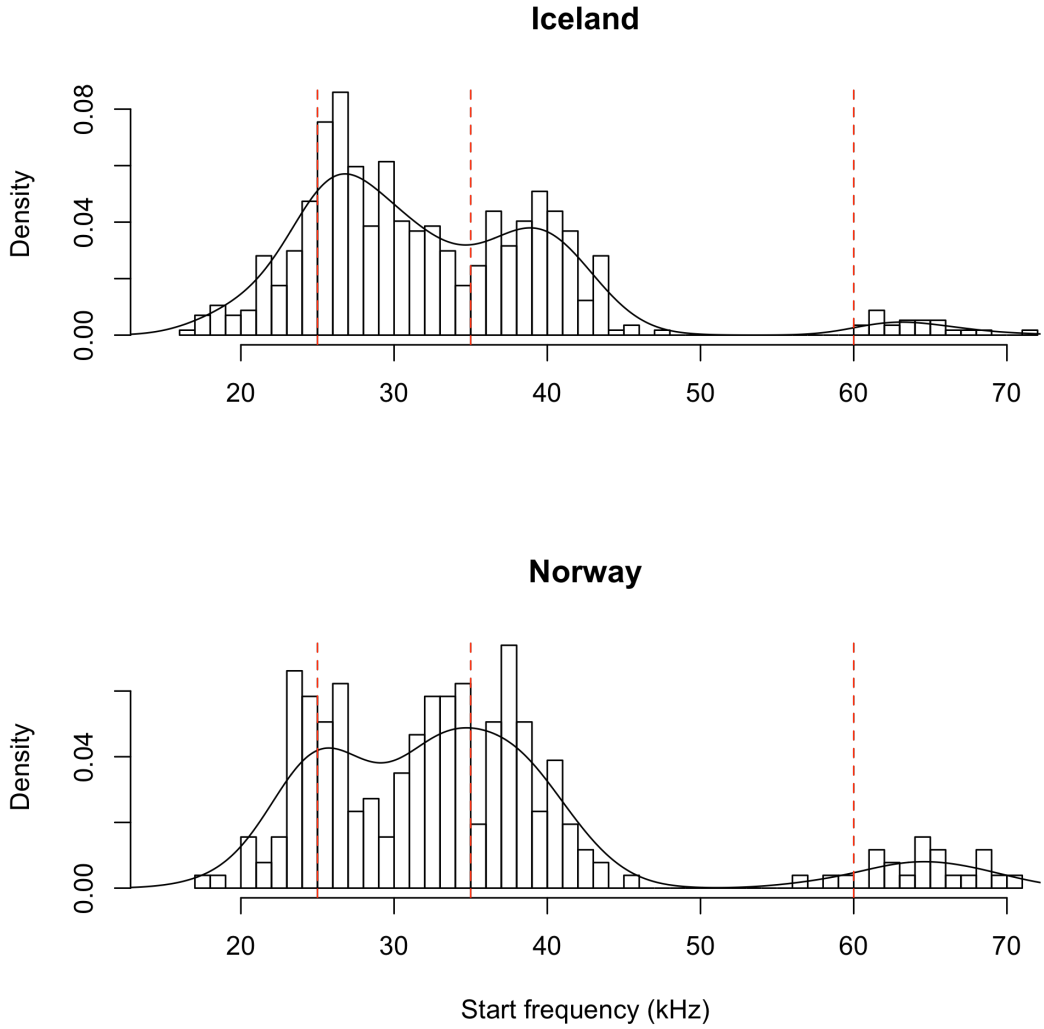


Figure A2-1. Distribution of start frequency measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 25, 35 and 60 kHz illustrate the difference in frequency of the modes from each population. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.8818, $p_{Iceland}$<0.001; W_{Norway}=0.8311, p_{Norway}<0.001)

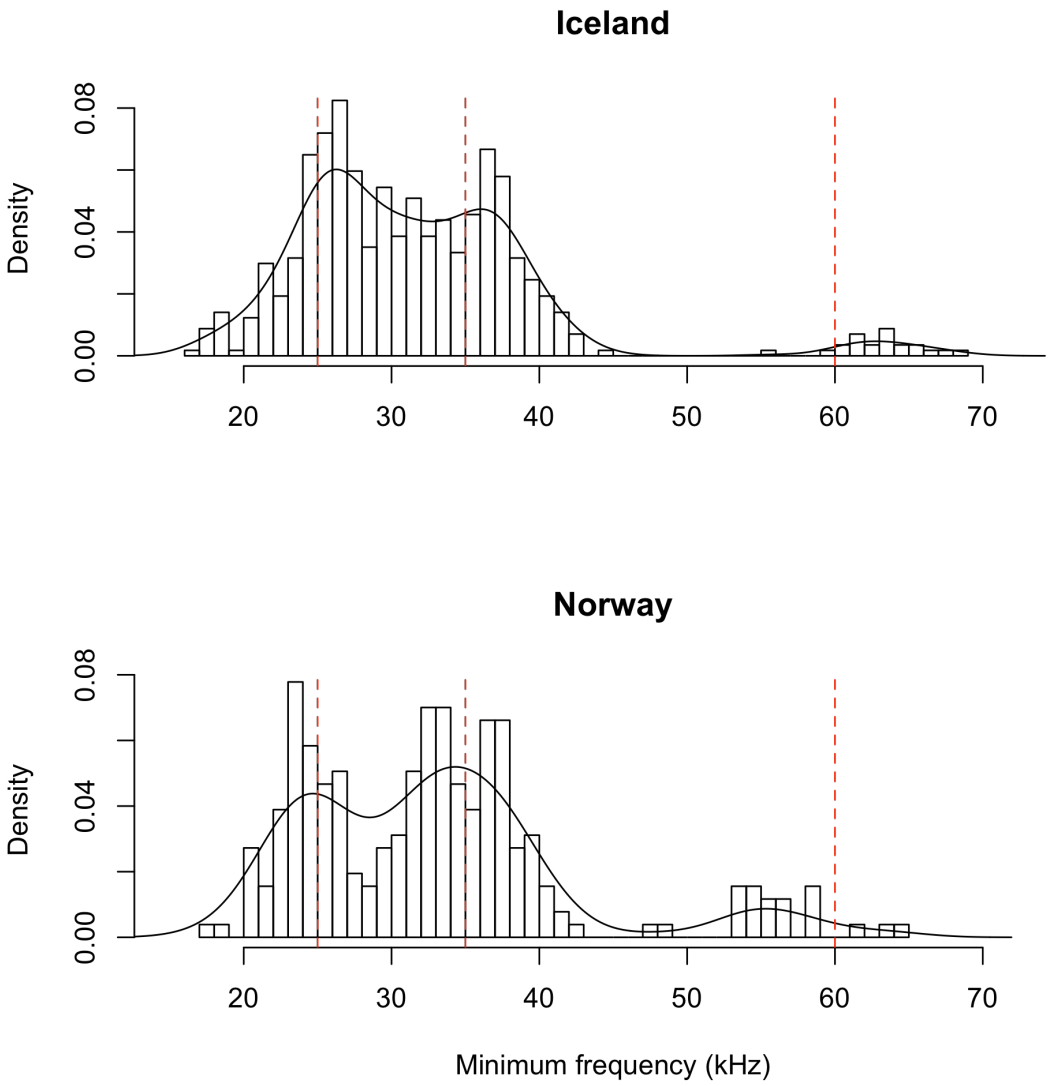


Figure A2-2. Distribution of minimum frequency measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 25, 35 and 60 kHz illustrate the difference in frequency of the modes from each population. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.8501, $p_{Iceland}$<0.001; W_{Norway}=0.8953, p_{Norway}<0.001)

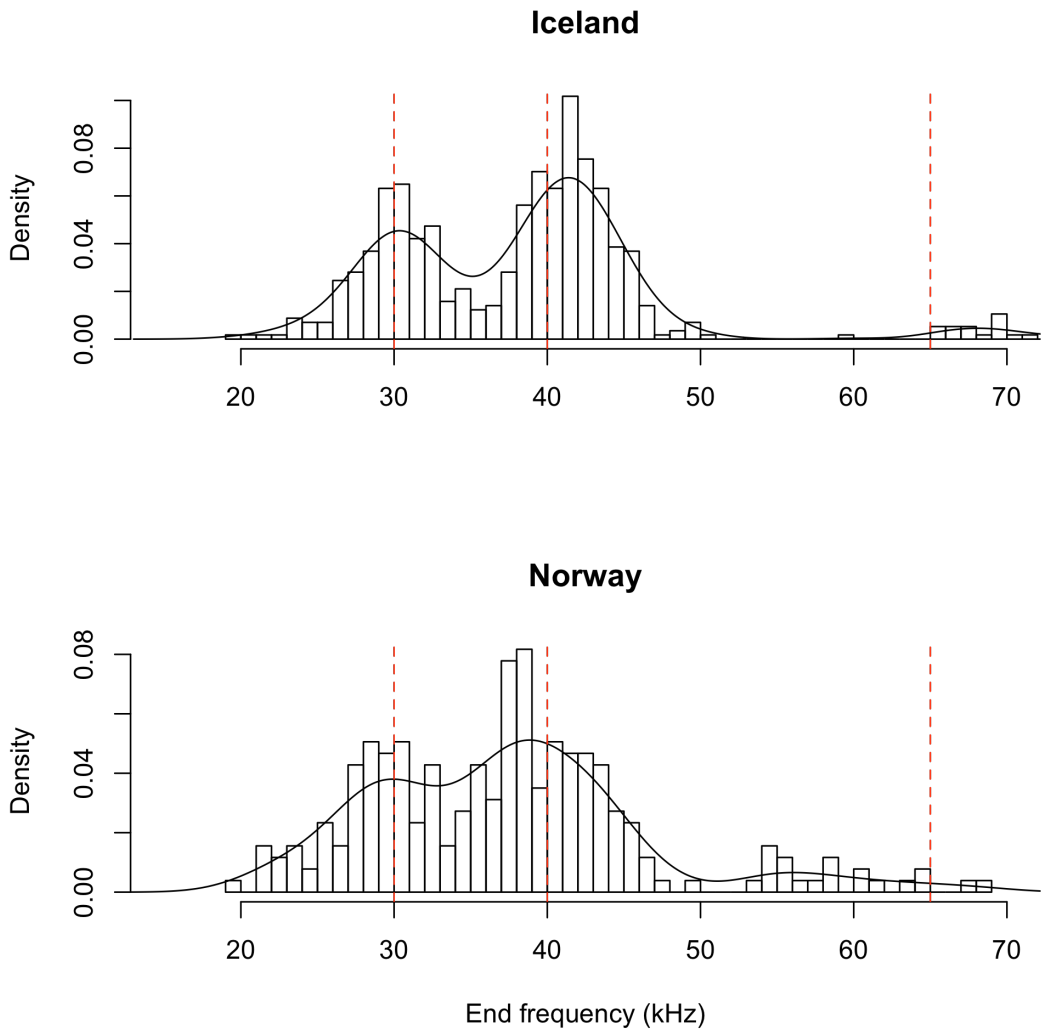


Figure A2-3. Distribution of end frequency measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 30, 40 and 65 kHz illustrate the difference in frequency of the modes from each population. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.8311, $p_{Iceland}$<0.001; W_{Norway}=0.9428, p_{Norway}<0.001)

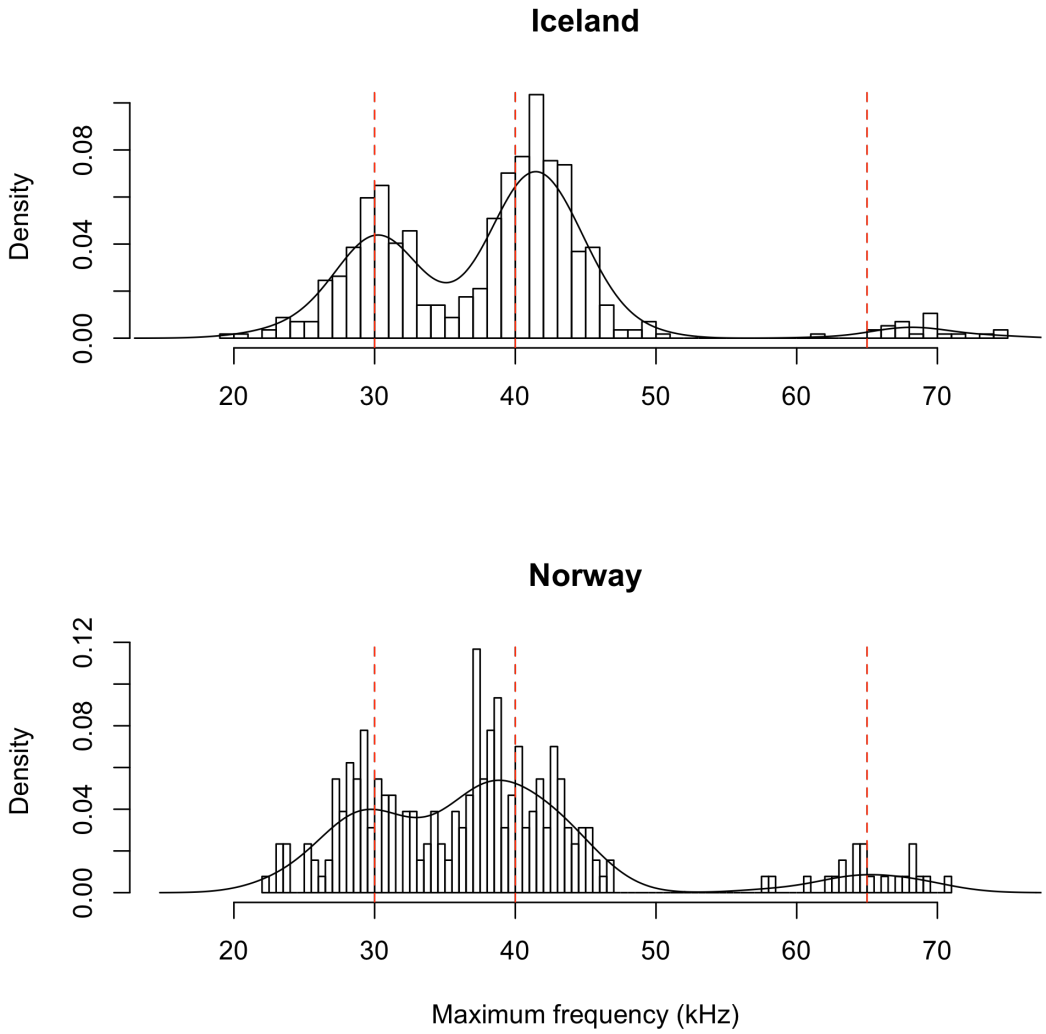


Figure A2-4. Distribution of maximum frequency measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 30, 40 and 65 kHz illustrate the difference in frequency of the modes from each population. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.8725, $p_{Iceland}$<0.001; W_{Norway}=0.861, p_{Norway}<0.001)

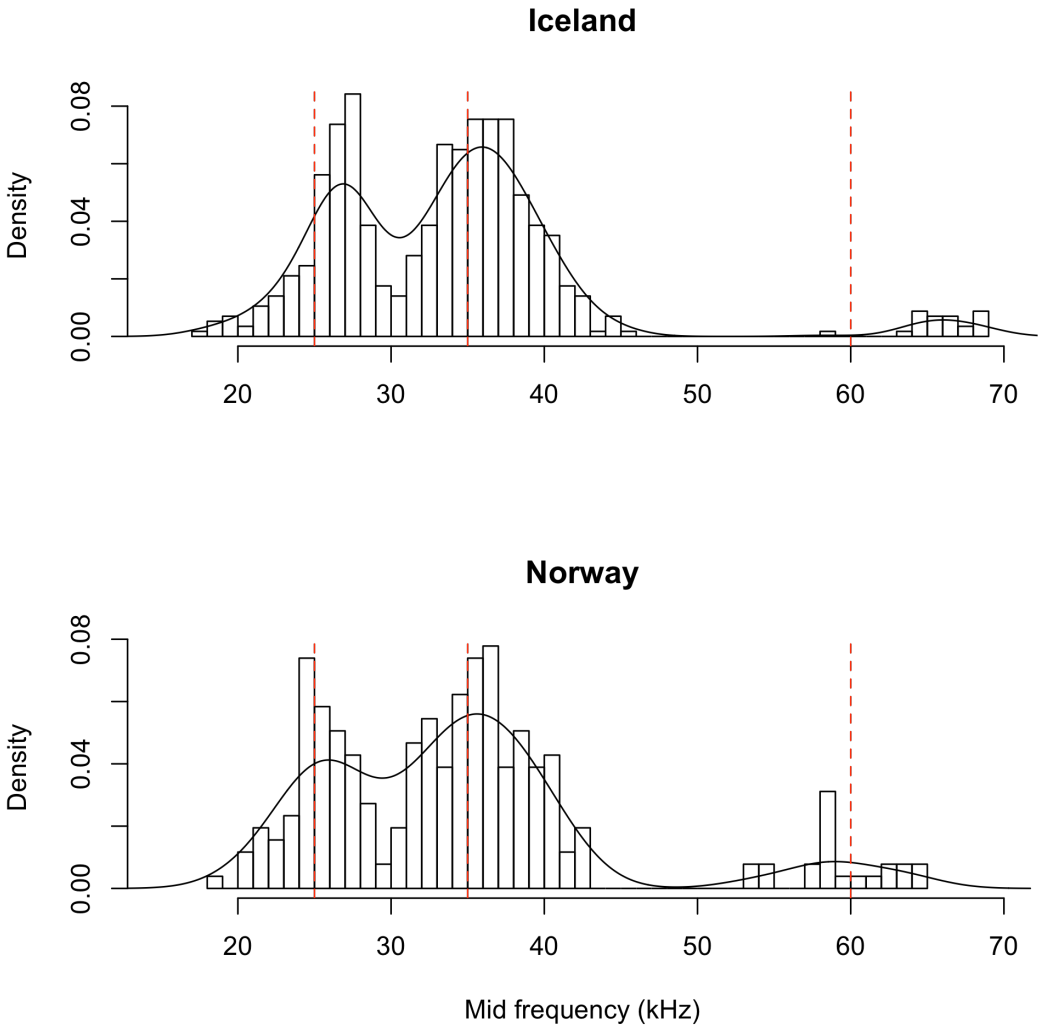


Figure A2-5. Distribution of mid frequency measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 25, 35 and 60 kHz illustrate the difference in frequency of the modes from each population. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.834, $p_{Iceland}$<0.001; W_{Norway}=0.873, p_{Norway}<0.001)

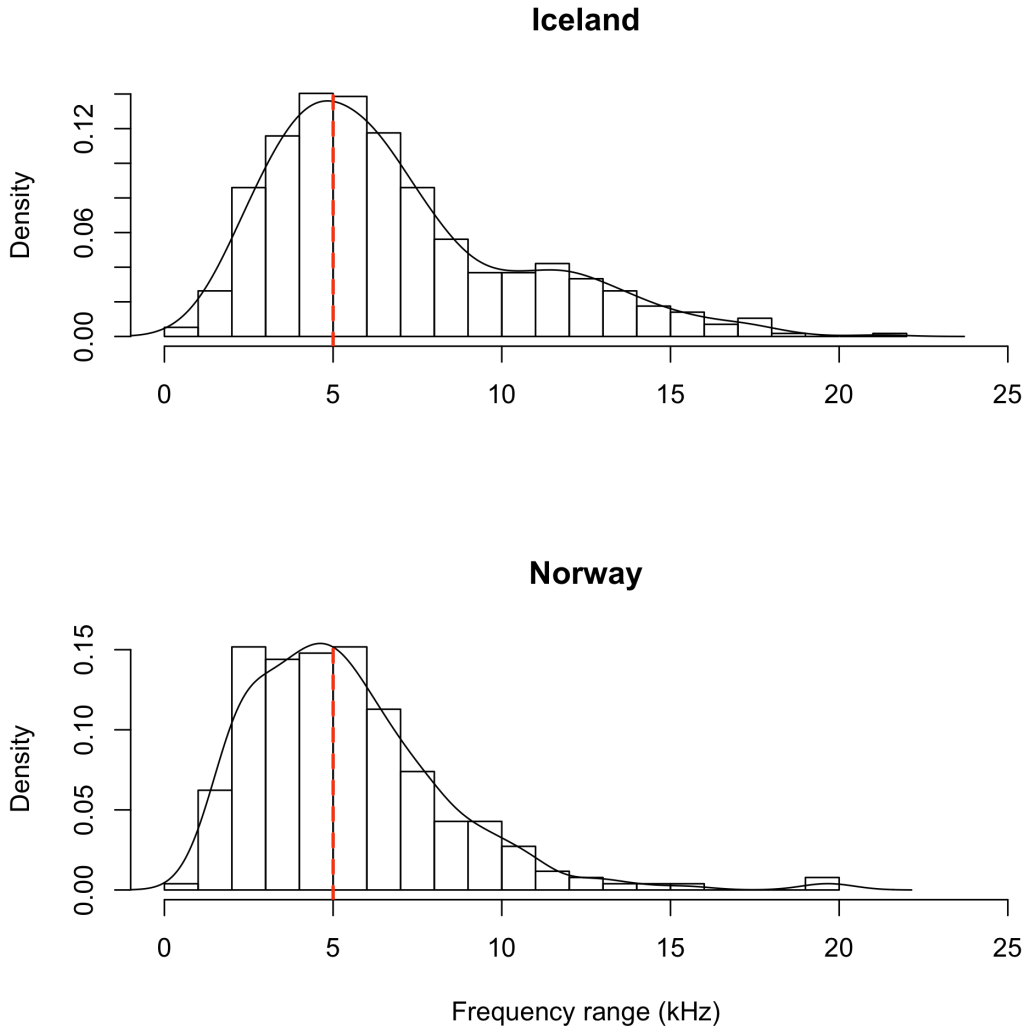


Figure A2-6. Distribution of frequency range measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed line at 5 kHz shows that both populations have a similar mode. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.9264, $p_{Iceland}$<0.001; W_{Norway}=0.902, p_{Norway}<0.001)

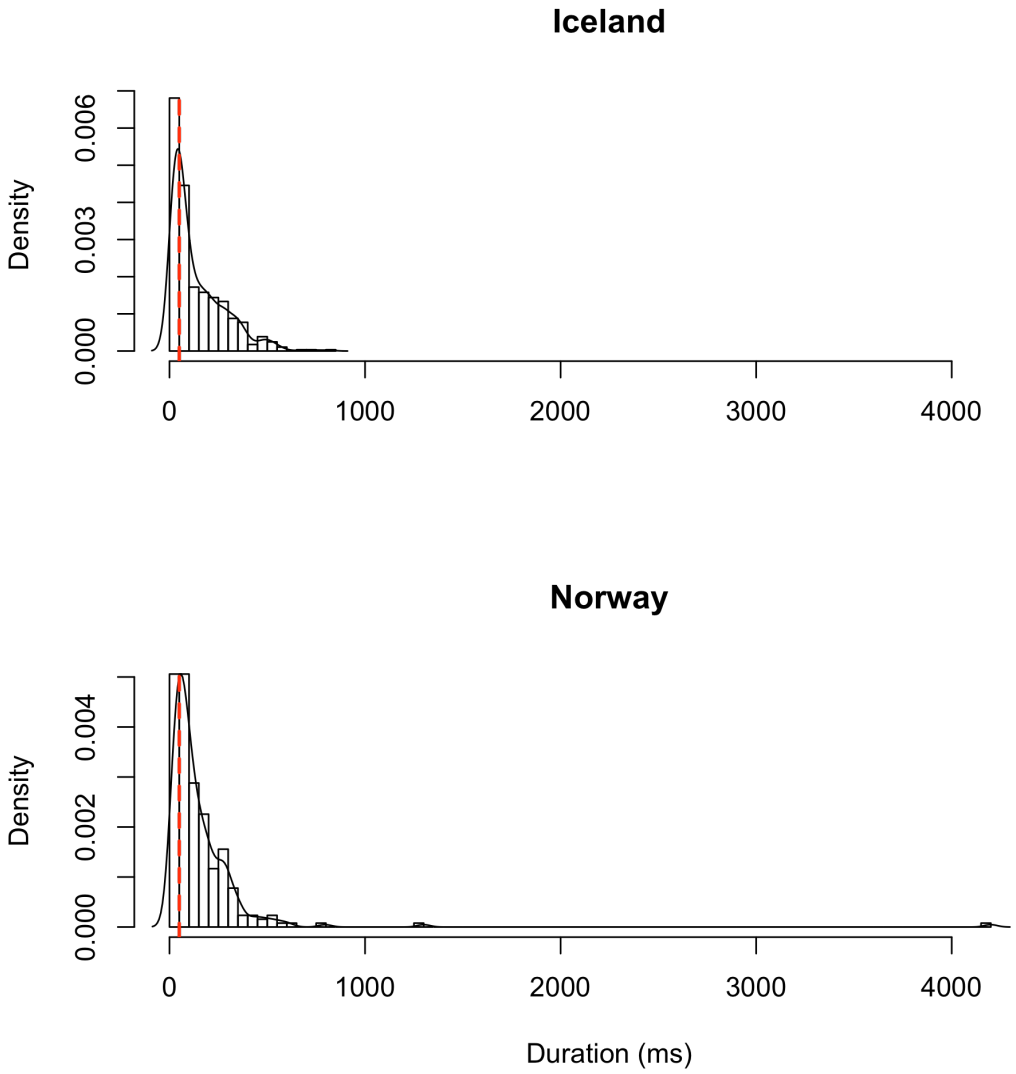
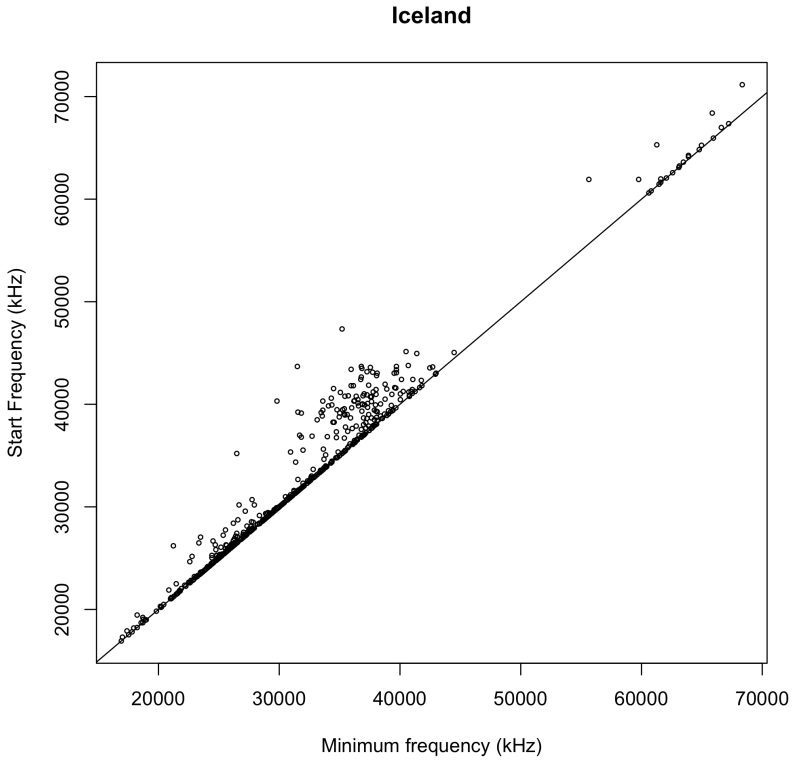
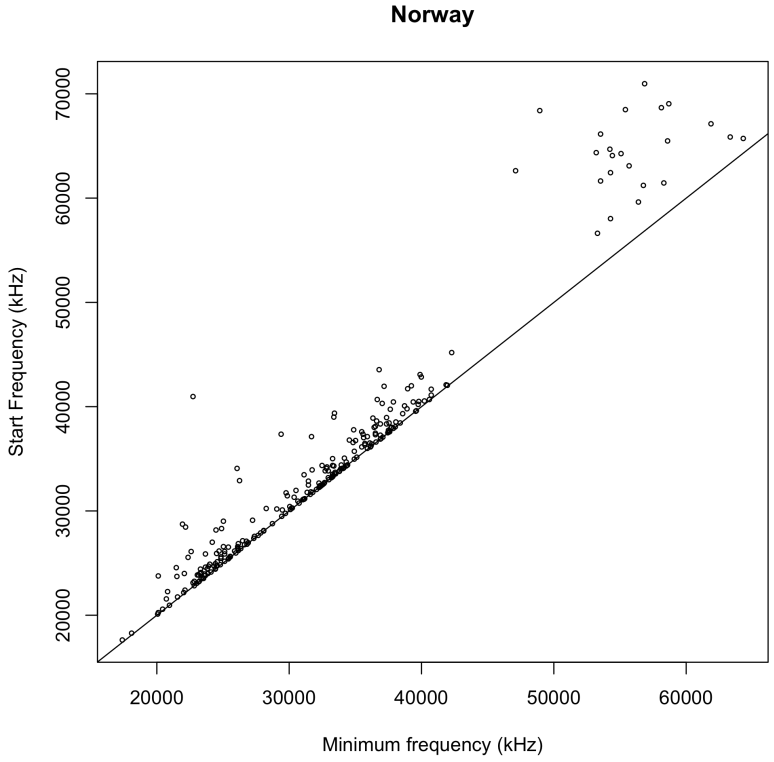


Figure A2-7. Distribution of duration measured from the fundamental frequency contours of all whistles from Iceland (n=570) and Norway (n=257) with overlapped Kernel density curve (black line). Red dashed lines at 100 ms shows that both populations have a similar mode. (Results of the Wilk-Shapiro normality tests: $W_{Iceland}$=0.8311, $p_{Iceland}$<0.001; W_{Norway}=0.3285, p_{Norway}<0.001)

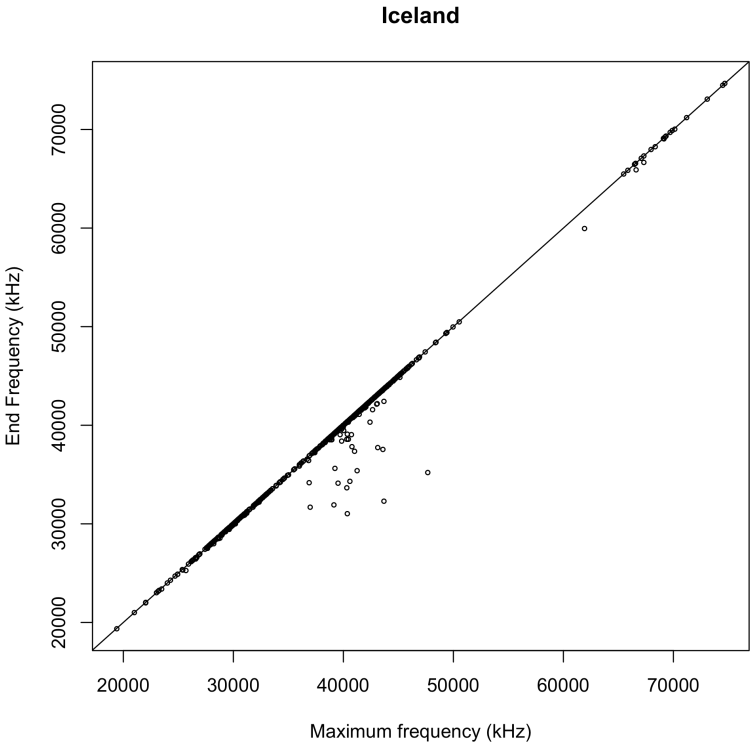


a)

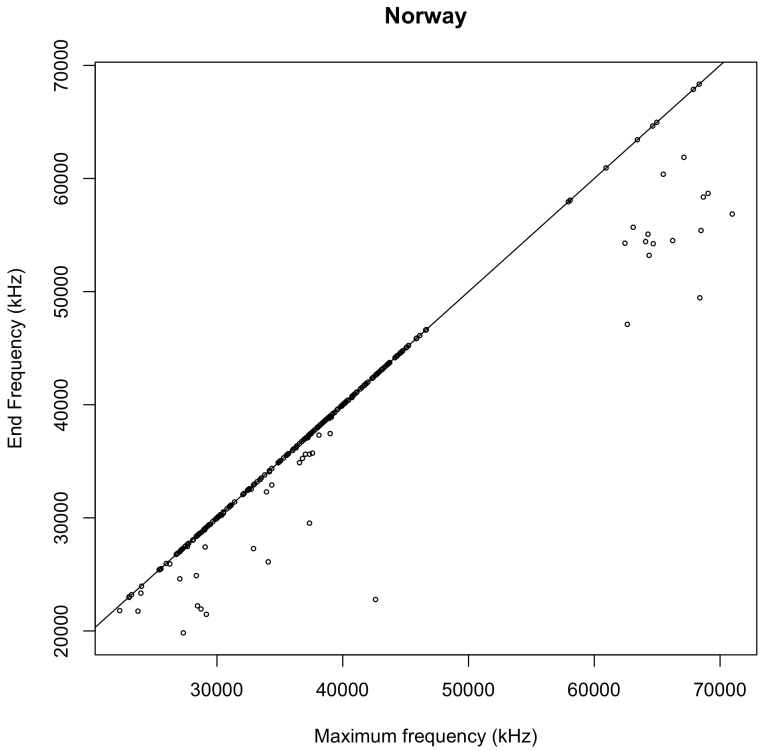


b)

Figure A2-8. Relationship between start and minimum frequency measured from the fundamental frequency contours of all whistles from: a) Iceland (*n*=570) and; b) Norway (*n*=257).



a)



b)

Figure A2-9. Relationship between end and maximum frequency measured from the fundamental frequency contours of all whistles from: a) Iceland (*n*=570) and; b) Norway (*n*=257).